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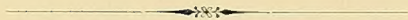
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# FORTEGNELSE

OVER

DET KONGELIGE DANSKE VIDENSKABERNES SELSKABS MEDLEMMER

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November 1923



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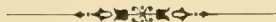


ON  
THE QUANTUM THEORY  
OF LINE-SPECTRA

BY

N. BOHR

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATHEM. AFD., 8. RÆKKE, IV. 1



KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL

BIANCO LUNOS BOGTRYKKERI

1918

*DEDICATED TO THE MEMORY OF MY VENERATED TEACHER*

*PROFESSOR C. CHRISTIANSEN*

*OCTOBER 9, 1843*

*† NOVEMBER 28, 1917*

UDGIVET PAA CARLSBERGFONDETS BEKOSTNING

## Introduction.

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In an attempt to develop certain outlines of a theory of line-spectra based on a suitable application of the fundamental ideas introduced by PLANCK in his theory of temperature-radiation to the theory of the nucleus atom of Sir ERNEST RUTHERFORD, the writer has shown that it is possible in this way to obtain a simple interpretation of some of the main laws governing the line-spectra of the elements, and especially to obtain a deduction of the well known Balmer formula for the hydrogen spectrum<sup>1)</sup>. The theory in the form given allowed of a detailed discussion only in the case of periodic systems, and obviously was not able to account in detail for the characteristic difference between the hydrogen spectrum and the spectra of other elements, or for the characteristic effects on the hydrogen spectrum of external electric and magnetic fields. Recently, however, a way out of this difficulty has been opened by SOMMERFELD<sup>2)</sup> who, by introducing a suitable generalisation of the theory to a simple type of non-periodic motions and by taking the small variation of the mass of the electron with its velocity into account, obtained an explanation of the fine-structure of the hydrogen lines which was found to be in brilliant conformity with the measurements. Already in his first paper on this subject, SOMMERFELD pointed out that his theory evidently offered a clue to the interpretation of the more intricate structure of the spectra of other elements. Briefly afterwards EPSTEIN<sup>3)</sup> and SCHWARZSCHILD<sup>4)</sup>, independent of each other, by adapting SOMMERFELD'S ideas to the treatment of a more extended class of non-periodic systems obtained a detailed explanation of the characteristic effect of an electric field on the hydrogen spectrum discovered by STARK. Subsequently SOMMERFELD<sup>5)</sup> himself and DEBYE<sup>6)</sup> have on the same lines indicated an interpretation of the

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<sup>1)</sup> N. BOHR, *Phil. Mag.*, XXVI, pp. 1, 476, 857 (1913), XXVII, p. 506 (1914), XXIX, p. 332 (1915), XXX, p. 394 (1915).

<sup>2)</sup> A. SOMMERFELD, *Ber. Akad. München*, 1915, pp. 425, 459, 1916, p. 131, 1917, p. 83. *Ann. de Phys.*, LI, p. 1 (1916).

<sup>3)</sup> P. EPSTEIN, *Phys. Zeitschr.* XVII, p. 148 (1916), *Ann. d. Phys.* L, p. 489, LI, p. 168 (1916).

<sup>4)</sup> K. SCHWARZSCHILD, *Ber. Akad. Berlin*, 1916, p. 548.

<sup>5)</sup> A. SOMMERFELD, *Phys. Zeitschr.* XVII, p. 491 (1916).

<sup>6)</sup> P. DEBYE, *Nachr. K. Ges. d. Wiss. Göttingen*, 1916, *Phys. Zeitschr.* XVII, p. 507 (1916).

effect of a magnetic field on the hydrogen spectrum which, although no complete explanation of the observations was obtained, undoubtedly represents an important step towards a detailed understanding of this phenomenon.

In spite of the great progress involved in these investigations many difficulties of fundamental nature remained unsolved, not only as regards the limited applicability of the methods used in calculating the frequencies of the spectrum of a given system, but especially as regards the question of the polarisation and intensity of the emitted spectral lines. These difficulties are intimately connected with the radical departure from the ordinary ideas of mechanics and electrodynamics involved in the main principles of the quantum theory, and with the fact that it has not been possible hitherto to replace these ideas by others forming an equally consistent and developed structure. Also in this respect, however, great progress has recently been obtained by the work of EINSTEIN<sup>1)</sup> and EHRENFEST<sup>2)</sup>. On this state of the theory it might therefore be of interest to make an attempt to discuss the different applications from a uniform point of view, and especially to consider the underlying assumptions in their relations to ordinary mechanics and electrodynamics. Such an attempt has been made in the present paper, and it will be shown that it seems possible to throw some light on the outstanding difficulties by trying to trace the analogy between the quantum theory and the ordinary theory of radiation as closely as possible.

The paper is divided into four parts.

- Part I contains a brief discussion of the general principles of the theory and deals with the application of the general theory to periodic systems of one degree of freedom and to the class of non-periodic systems referred to above.
- Part II contains a detailed discussion of the theory of the hydrogen spectrum in order to illustrate the general considerations.
- Part III contains a discussion of the questions arising in connection with the explanation of the spectra of other elements.
- Part IV contains a general discussion of the theory of the constitution of atoms and molecules based on the application of the quantum theory to the nucleus atom.

Copenhagen, November 1917.

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<sup>1)</sup> A. EINSTEIN, Verh. d. D. phys. Ges. XVIII, p. 318 (1916), Phys. Zeitschr. XVIII, p. 121 (1917).

<sup>2)</sup> P. EHRENFEST, Proc. Acad. Amsterdam, XVI, p. 591 (1914), Phys. Zeitschr. XV, p. 657 (1914), Ann. d. Phys. LI, p. 327 (1916) Phil. Mag. XXXIII, p. 500 (1917).

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## Part I.

### On the general theory.

#### § 1. General principles.

The quantum theory of line-spectra rests upon the following fundamental assumptions:

I. That an atomic system can, and can only, exist permanently in a certain series of states corresponding to a discontinuous series of values for its energy, and that consequently any change of the energy of the system, including emission and absorption of electromagnetic radiation, must take place by a complete transition between two such states. These states will be denoted as the "stationary states" of the system.

II. That the radiation absorbed or emitted during a transition between two stationary states is "unifrequent" and possesses a frequency  $\nu$ , given by the relation

$$E' - E'' = h\nu, \quad (1)$$

where  $h$  is PLANCK's constant and where  $E'$  and  $E''$  are the values of the energy in the two states under consideration.

As pointed out by the writer in the papers referred to in the introduction, these assumptions offer an immediate interpretation of the fundamental principle of combination of spectral lines deduced from the measurements of the frequencies of the series spectra of the elements. According to the laws discovered by BALMER, RYDBERG and RITZ, the frequencies of the lines of the series spectrum of an element can be expressed by a formula of the type:

$$\nu = f_{\tau''}(n'') - f_{\tau'}(n'), \quad (2)$$

where  $n'$  and  $n''$  are whole numbers and  $f_{\tau}(n)$  is one among a set of functions of  $n$ , characteristic for the element under consideration. On the above assumptions this formula may obviously be interpreted by assuming that the stationary states of an atom of an element form a set of series, and that the energy in the  $n^{\text{th}}$  state of the  $\tau^{\text{th}}$  series, omitting an arbitrary constant, is given by

$$E_{\tau}(n) = -hf_{\tau}(n). \quad (3)$$

We thus see that the values for the energy in the stationary states of an atom may be obtained directly from the measurements of the spectrum by means of relation (1). In order, however, to obtain a theoretical connection between these

values and the experimental evidence about the constitution of the atom obtained from other sources, it is necessary to introduce further assumptions about the laws which govern the stationary states of a given atomic system and the transitions between these states.

Now on the basis of a vast amount of experimental evidence, we are forced to assume that an atom or molecule consists of a number of electrified particles in motion, and, since the above fundamental assumptions imply that no emission of radiation takes place in the stationary states, we must consequently assume that the ordinary laws of electrodynamics cannot be applied to these states without radical alterations. In many cases, however, the effect of that part of the electrodynamical forces which is connected with the emission of radiation will at any moment be very small in comparison with the effect of the simple electrostatic attractions or repulsions of the charged particles corresponding to COULOMB'S law. Even if the theory of radiation must be completely altered, it is therefore a natural assumption that it is possible in such cases to obtain a close approximation in the description of the motion in the stationary states, by retaining only the latter forces. In the following we shall therefore, as in all the papers mentioned in the introduction, for the present calculate the motions of the particles in the stationary states as the motions of mass-points according to ordinary mechanics including the modifications claimed by the theory of relativity, and we shall later in the discussion of the special applications come back to the question of the degree of approximation which may be obtained in this way.

If next we consider a transition between two stationary states, it is obvious at once from the essential discontinuity, involved in the assumptions I and II, that in general it is impossible even approximately to describe this phenomenon by means of ordinary mechanics or to calculate the frequency of the radiation absorbed or emitted by such a process by means of ordinary electrodynamics. On the other hand, from the fact that it has been possible by means of ordinary mechanics and electrodynamics to account for the phenomenon of temperature-radiation in the limiting region of slow vibrations, we may expect that any theory capable of describing this phenomenon in accordance with observations will form some sort of natural generalisation of the ordinary theory of radiation. Now the theory of temperature-radiation in the form originally given by PLANCK confessedly lacked internal consistency, since, in the deduction of his radiation formula, assumptions of similar character as I and II were used in connection with assumptions which were in obvious contrast to them. Quite recently, however, EINSTEIN<sup>1)</sup> has succeeded, on the basis of the assumptions I and II, to give a consistent and instructive deduction of PLANCK'S formula by introducing certain supplementary assumptions about the probability of transition of a system between two stationary states and about the manner in which this probability depends on the density of radia-

<sup>1)</sup> A. EINSTEIN, loc. cit.

tion of the corresponding frequency in the surrounding space, suggested from analogy with the ordinary theory of radiation. EINSTEIN compares the emission or absorption of radiation of frequency  $\nu$  corresponding to a transition between two stationary states with the emission or absorption to be expected on ordinary electrodynamics for a system consisting of a particle executing harmonic vibrations of this frequency. In analogy with the fact that on the latter theory such a system will without external excitation emit a radiation of frequency  $\nu$ , EINSTEIN assumes in the first place that on the quantum theory there will be a certain probability  $A_{n''}^{n'} dt$  that the system in the stationary state of greater energy, characterised by the letter  $n'$ , in the time interval  $dt$  will start spontaneously to pass to the stationary state of smaller energy, characterised by the letter  $n''$ . Moreover, on ordinary electrodynamics the harmonic vibrator will, in addition to the above mentioned independent emission, in the presence of a radiation of frequency  $\nu$  in the surrounding space, and dependent on the accidental phase-difference between this radiation and the vibrator, emit or absorb radiation-energy. In analogy with this, EINSTEIN assumes secondly that in the presence of a radiation in the surrounding space, the system will on the quantum theory, in addition to the above mentioned probability of spontaneous transition from the state  $n'$  to the state  $n''$ , possess a certain probability, depending on this radiation, of passing in the time  $dt$  from the state  $n'$  to the state  $n''$ , as well as from the state  $n''$  to the state  $n'$ . These latter probabilities are assumed to be proportional to the intensity of the surrounding radiation and are denoted by  $\rho_\nu B_{n''}^{n'} dt$  and  $\rho_\nu B_{n'}^{n''} dt$  respectively, where  $\rho_\nu d\nu$  denotes the amount of radiation in unit volume of the surrounding space distributed on frequencies between  $\nu$  and  $\nu + d\nu$ , while  $B_{n''}^{n'}$  and  $B_{n'}^{n''}$  are constants which, like  $A_{n''}^{n'}$ , depend only on the stationary states under consideration. EINSTEIN does not introduce any detailed assumption as to the values of these constants, no more than to the conditions by which the different stationary states of a given system are determined or to the "a-priori probability" of these states on which their relative occurrence in a distribution of statistical equilibrium depends. He shows, however, how it is possible from the above general assumptions, by means of BOLTZMANN'S principle on the relation between entropy and probability and WIEN'S well known displacement-law, to deduce a formula for the temperature radiation which apart from an undetermined constant factor coincides with PLANCK'S, if we only assume that the frequency corresponding to the transition between the two states is determined by (1). It will therefore be seen that by reversing the line of argument, EINSTEIN'S theory may be considered as a very direct support of the latter relation.

In the following discussion of the application of the quantum theory to determine the line-spectrum of a given system, it will, just as in the theory of temperature-radiation, not be necessary to introduce detailed assumptions as to the mechanism of transition between two stationary states. We shall show, however, that the conditions which will be used to determine the values of the energy in the stationary states are of such a type that the frequencies calculated by (1), in the limit



where the motions in successive stationary states comparatively differ very little from each other, will tend to coincide with the frequencies to be expected on the ordinary theory of radiation from the motion of the system in the stationary states. In order to obtain the necessary relation to the ordinary theory of radiation in the limit of slow vibrations, we are therefore led directly to certain conclusions about the probability of transition between two stationary states in this limit. This leads again to certain general considerations about the connection between the probability of a transition between any two stationary states and the motion of the system in these states, which will be shown to throw light on the question of the polarisation and intensity of the different lines of the spectrum of a given system.

In the above considerations we have by an atomic system tacitly understood a number of electrified particles which move in a field of force which, with the approximation mentioned, possesses a potential depending only on the position of the particles. This may more accurately be denoted as a system under constant external conditions, and the question next arises about the variation in the stationary states which may be expected to take place during a variation of the external conditions, e. g. when exposing the atomic system to some variable external field of force. Now, in general, we must obviously assume that this variation cannot be calculated by ordinary mechanics, no more than the transition between two different stationary states corresponding to constant external conditions. If, however, the variation of the external conditions is very slow, we may from the necessary stability of the stationary states expect that the motion of the system at any given moment during the variation will differ only very little from the motion in a stationary state corresponding to the instantaneous external conditions. If now, moreover, the variation is performed at a constant or very slowly changing rate, the forces to which the particles of the system will be exposed will not differ at any moment from those to which they would be exposed if we imagine that the external forces arise from a number of slowly moving additional particles which together with the original system form a system in a stationary state. From this point of view it seems therefore natural to assume that, with the approximation mentioned, the motion of an atomic system in the stationary states can be calculated by direct application of ordinary mechanics, not only under constant external conditions, but in general also during a slow and uniform variation of these conditions. This assumption, which may be denoted as the principle of the „mechanical transformability” of the stationary states, has been introduced in the quantum theory by EHRENFEST<sup>1)</sup> and is, as it will be seen in the following sections, of great importance in the discussion of the conditions to be used to fix

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<sup>1)</sup> P. EHRENFEST, loc. cit. In these papers the principle in question is called the “adiabatic hypothesis” in accordance with the line of argumentation followed by EHRENFEST in which considerations of thermodynamical problems play an important part. From the point of view taken in the present paper, however, the above notation might in a more direct way indicate the content of the principle and the limits of its applicability.



the stationary states of an atomic system among the continuous multitude of mechanically possible motions. In this connection it may be pointed out that the principle of the mechanical transformability of the stationary states allows us to overcome a fundamental difficulty which at first sight would seem to be involved in the definition of the energy difference between two stationary states which enters in relation (1). In fact we have assumed that the direct transition between two such states cannot be described by ordinary mechanics, while on the other hand we possess no means of defining an energy difference between two states if there exists no possibility for a continuous mechanical connection between them. It is clear, however, that such a connection is just afforded by EHRENFEST's principle which allows us to transform mechanically the stationary states of a given system into those of another, because for the latter system we may take one in which the forces which act on the particles are very small and where we may assume that the values of the energy in all the stationary states will tend to coincide.

As regards the problem of the statistical distribution of the different stationary states between a great number of atomic systems of the same kind in temperature equilibrium, the number of systems present in the different states may be deduced in the well known way from BOLTZMANN's fundamental relation between entropy and probability, if we know the values of the energy in these states and the a-priori probability to be ascribed to each state in the calculation of the probability of the whole distribution. In contrast to considerations of ordinary statistical mechanics we possess on the quantum theory no direct means of determining these a-priori probabilities, because we have no detailed information about the mechanism of transition between the different stationary states. If the a-priori probabilities are known for the states of a given atomic system, however, they may be deduced for any other system which can be formed from this by a continuous transformation without passing through one of the singular systems referred to below. In fact, in examining the necessary conditions for the explanation of the second law of thermodynamics EHRENFEST<sup>1)</sup> has deduced a certain general condition as regards the variation of the a-priori probability corresponding to a small change of the external conditions from which it follows, that the a-priori probability of a given stationary state of an atomic system must remain unaltered during a continuous transformation, except in special cases in which the values of the energy in some of the stationary states will tend to coincide during the transformation. In this result we possess, as we shall see, a rational basis for the determination of the a-priori probability of the different stationary states of a given atomic system.

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<sup>1)</sup> P. EHRENFEST, Phys. Zeitschr. XV p. 660 (1914). The above interpretation of this relation is not stated explicitly by EHRENFEST, but it presents itself directly if the quantum theory is taken in the form corresponding to the fundamental assumption I.

## § 2. Systems of one degree of freedom.

As the simplest illustration of the principles discussed in the former section we shall begin by considering systems of a single degree of freedom, in which case it has been possible to establish a general theory of stationary states. This is due to the fact, that the motion will be simply periodic, provided the distance between the parts of the system will not increase infinitely with the time, a case which for obvious reasons cannot represent a stationary state in the sense defined above. On account of this, the discussion of the mechanical transformability of the stationary states can, as pointed out by EHRENFEST<sup>1)</sup>, for systems of one degree of freedom be based on a mechanical theorem about periodic systems due to BOLTZMANN and originally applied by this author in a discussion of the bearing of mechanics on the explanation of the laws of thermodynamics. For the sake of the considerations in the following sections it will be convenient here to give the proof in a form which differs slightly from that given by EHRENFEST, and which takes also regard to the modifications in the ordinary laws of mechanics claimed by the theory of relativity.

Consider for the sake of generality a conservative mechanical system of  $s$  degrees of freedom, the motion of which is governed by HAMILTON's equations:

$$\frac{dp_k}{dt} = -\frac{\partial E}{\partial q_k}, \quad \frac{dq_k}{dt} = \frac{\partial E}{\partial p_k}, \quad (k = 1, \dots, s) \quad (4)$$

where  $E$  is the total energy considered as a function of the generalised positional coordinates  $q_1, \dots, q_s$  and the corresponding canonically conjugated momenta  $p_1, \dots, p_s$ . If the velocities are so small that the variation in the mass of the particles due to their velocities can be neglected, the  $p$ 's are defined in the usual way by

$$p_k = \frac{\partial T}{\partial \dot{q}_k}, \quad (k = 1, \dots, s)$$

where  $T$  is the kinetic energy of the system considered as a function of the generalised velocities  $\dot{q}_1, \dots, \dot{q}_s$  ( $\dot{q}_k = \frac{dq_k}{dt}$ ) and of  $q_1, \dots, q_s$ . If the relativity modifications are taken into account the  $p$ 's are defined by a similar set of expressions in which the kinetic energy is replaced by  $T' = \sum m_0 c^2 (1 - \sqrt{1 - v^2/c^2})$ , where the summation is to be extended over all the particles of the system, and  $v$  is the velocity of one of the particles and  $m_0$  its mass for zero velocity, while  $c$  is the velocity of light.

Let us now assume that the system performs a periodic motion with the period  $\sigma$ , and let us form the expression

$$I = \int_0^\sigma \sum_{k=1}^s p_k \dot{q}_k dt, \quad (5)$$

<sup>1)</sup> P. EHRENFEST, loc. cit. Proc. Acad. Amsterdam, XVI, p. 591 (1914).

which is easily seen to be independent of the special choice of coordinates  $q_1, \dots, q_s$  used to describe the motion of the system. In fact, if the variation of the mass with the velocity is neglected we get

$$I = 2 \int_0^\sigma T dt,$$

and if the relativity modifications are included, we get a quite analogous expression in which the kinetic energy is replaced by  $T'' = \frac{1}{2} m_0 v^2 / \sqrt{1 - v^2/c^2}$ .

Consider next some new periodic motion of the system formed by a small variation of the first motion, but which may need the presence of external forces in order to be a mechanically possible motion. For the variation in  $I$  we get then

$$\delta I = \int_0^\sigma \sum_1^s (\dot{q}_k \delta p_k + p_k \delta \dot{q}_k) dt + \left| \sum_1^s p_k \dot{q}_k \delta t \right|_0^\sigma,$$

where the last term refers to the variation of the limit of the integral due to the variation in the period  $\sigma$ . By partial integration of the second term in the bracket under the integral we get next

$$\delta I = \int_0^\sigma \sum_1^s (\dot{q}_k \delta p_k - \dot{p}_k \delta q_k) dt + \left| \sum_1^s p_k (\dot{q}_k \delta t + \delta q_k) \right|_0^\sigma,$$

where the last term is seen to be zero, because the term in the bracket as well as  $p_k$  will be the same in both limits, since the varied motion as well as the original motion is assumed to be periodic. By means of equations (4) we get therefore

$$\delta I = \int_0^\sigma \sum_1^s \left( \frac{\partial E}{\partial p_k} \delta p_k + \frac{\partial E}{\partial q_k} \delta q_k \right) dt = \int_0^\sigma \delta E dt. \quad (6)$$

Let us now assume that the small variation of the motion is produced by a small external field established at a uniform rate during a time interval  $\vartheta$ , long compared with  $\sigma$ , so that the comparative increase during a period is very small. In this case  $\delta E$  is at any moment equal to the total work done by the external forces on the particles of the system since the beginning of the establishment of the field. Let this moment be  $t = -\vartheta$  and let the potential of the external field at  $t \geq 0$  be given by  $\mathcal{Q}$ , expressed as a function of the  $q$ 's. At any given moment  $t > 0$  we have then

$$\delta E = - \int_{-\vartheta}^0 \frac{\partial \mathcal{Q}}{\partial t} dt - \sum_1^s \frac{\partial \mathcal{Q}}{\partial q_k} \dot{q}_k dt - \int_0^t \sum_1^s \frac{\partial \mathcal{Q}}{\partial q_k} \dot{q}_k dt,$$

which gives by partial integration



$$\delta E = \frac{1}{\bar{q}} \int_{-\bar{q}}^{\bar{q}} \mathcal{Q} dt - \mathcal{Q}_t,$$

where the values for the  $q$ 's to be introduced in  $\mathcal{Q}$  in the first term are those corresponding to the motion under the influence of the increasing external field, and the values to be introduced in the second term are those corresponding to the configuration at the time  $t$ . Neglecting small quantities of the same order as the square of the external force, however, we may in this expression for  $\delta E$  instead of the values for the  $q$ 's corresponding to the perturbed motion take those corresponding to the original motion of the system. With this approximation the first term is equal to the mean value of the second taken over a period  $\sigma$ , and we have consequently

$$\int_0^\sigma \delta E dt = 0. \quad (7)$$

From (6) and (7) it follows that  $I$  will remain constant during the slow establishment of the small external field, if the motion corresponding to a constant value of the field is periodic. If next the external field corresponding to  $\mathcal{Q}$  is considered as an inherent part of the system, it will be seen in the same way that  $I$  will remain unaltered during the establishment of a new small external field, and so on. Consequently  $I$  will be invariant for any finite transformation of the system which is sufficiently slowly performed, provided the motion at any moment during the process is periodic and the effect of the variation is calculated on ordinary mechanics.

Before we proceed to the applications of this result we shall mention a simple consequence of (6) for systems for which every orbit is periodic independent of the initial conditions. In that case we may for the varied motion take an undisturbed motion of the system corresponding to slightly different initial conditions. This gives  $\delta E$  constant, and from (6) we get therefore

$$\delta E = \omega \delta I, \quad (8)$$

where  $\omega = \frac{1}{\sigma}$  is the frequency of the motion. This equation forms a simple relation between the variations in  $E$  and  $I$  for periodic systems, which will be often used in the following.

Returning now to systems of one degree of freedom, we shall take our starting point from PLANCK's original theory of a linear harmonic vibrator. According to this theory the stationary states of a system, consisting of a particle executing linear harmonic vibrations with a constant frequency  $\omega_0$  independent of the energy, are given by the well known relation

$$E = nh\omega_0, \quad (9)$$

where  $n$  is a positive entire number,  $h$  PLANCK's constant, and  $E$  the total energy which is supposed to be zero if the particle is at rest.



From (8) it follows at once, that (9) is equivalent to

$$I = \int_0^\sigma p \dot{q} dt = \int p dq = nh, \quad (10)$$

where the latter integral is to be taken over a complete oscillation of  $q$  between its limits. On the principle of the mechanical transformability of the stationary states we shall therefore assume, following EHRENFEST, that (10) holds not only for a PLANCK's vibrator but for any periodic system of one degree of freedom which can be formed in a continuous manner from a linear harmonic vibrator by a gradual variation of the field of force in which the particle moves. This condition is immediately seen to be fulfilled by all such systems in which the motion is of oscillating type i. e. where the moving particle during a period passes twice through any point of its orbit once in each direction. If, however, we confine ourselves to systems of one degree of freedom, it will be seen that systems in which the motion is of rotating type, i. e. where the particle during a period passes only once through every point of its orbit, cannot be formed in a continuous manner from a linear harmonic vibrator without passing through singular states in which the period becomes infinite long and the result becomes ambiguous. We shall not here enter more closely on this difficulty which has been pointed out by EHRENFEST, because it disappears when we consider systems of several degrees of freedom, where we shall see that a simple generalisation of (10) holds for any system for which every motion is periodic.

As regards the application of (9) to statistical problems it was assumed in PLANCK's theory that the different states of the vibrator corresponding to different values of  $n$  are a-priori equally probable, and this assumption was strongly supported by the agreement obtained on this basis with the measurements of the specific heat of solids at low temperatures. Now it follows from the considerations of EHRENFEST, mentioned in the former section, that the a-priori probability of a given stationary state is not changed by a continuous transformation, and we shall therefore expect that for any system of one degree of freedom the different states corresponding to different entire values of  $n$  in (10) are a-priori equally probable.

As pointed out by PLANCK in connection with the application of (9), it is simply seen that statistical considerations, based on the assumption of equal probability for the different states given by (10), will show the necessary relation to considerations of ordinary statistical mechanics in the limit where the latter theory has been found to give results in agreement with experiments. Let the configuration and motion of a mechanical system be characterised by  $s$  independent variables  $q_1, \dots, q_s$  and corresponding momenta  $p_1, \dots, p_s$ , and let the state of the system be represented in a  $2s$ -dimensional phase-space by a point with coordinates  $q_1, \dots, q_s, p_1, \dots, p_s$ . Then, according to ordinary statistical mechanics, the probability for this point to lie within a small element in the phase-space is independent of the

position and shape of this element and simply proportional to its volume, defined in the usual way by

$$\delta W = \int dq_1 \dots dq_s dp_1 \dots dp_s. \quad (11)$$

In the quantum theory, however, these considerations cannot be directly applied, since the point representing the state of a system cannot be displaced continuously in the  $2s$ -dimensional phase-space, but can lie only on certain surfaces of lower dimensions in this space. For systems of one degree of freedom the phase-space is a two-dimensional surface, and the points representing the states of some system given by (10) will be situated on closed curves on this surface. Now, in general, the motion will differ considerably for any two states corresponding to successive entire values of  $n$  in (10), and a simple general connection between the quantum theory and ordinary statistical mechanics is therefore out of question. In the limit, however, where  $n$  is large, the motions in successive states will only differ very little from each other, and it would therefore make little difference whether the points representing the systems are distributed continuously on the phase-surface or situated only on the curves corresponding to (10), provided the number of systems which in the first case are situated between two such curves is equal to the number which in the second case lies on one of these curves. But it will be seen that this condition is just fulfilled in consequence of the above hypothesis of equal a-priori probability of the different stationary states, because the element of phase-surface limited by two successive curves corresponding to (10) is equal to

$$\delta W = \int dp dq = \left[ \int p dq \right]_n - \left[ \int p dq \right]_{n-1} = I_n - I_{n-1} = h, \quad (12)$$

so that on ordinary statistical mechanics the probabilities for the point to lie within any two such elements is the same. We see consequently that the hypothesis of equal probability of the different states given by (10) gives the same result as ordinary statistical mechanics in all such applications in which the states of the great majority of the systems correspond to large values of  $n$ . Considerations of this kind have led DEBYE<sup>1)</sup> to point out that condition (10) might have a general validity for systems of one degree of freedom, already before EHRENFEST, on the basis of his theory of the mechanical transformability of the stationary states, had shown that this condition forms the only rational generalisation of PLANCK's condition (9).

We shall now discuss the relation between the theory of spectra of atomic systems of one degree of freedom, based on (1) and (10), and the ordinary theory of radiation, and we shall see that this relation in several respects shows a close analogy to the relation, just considered, between the statistical applications of (10) and considerations based on ordinary statistical mechanics. Since the values

<sup>1)</sup> P. DEBYE, Wolfskehl-Vortrag. Göttingen (1913).

for the frequency  $\omega$  in two states corresponding to different values of  $n$  in (10) in general are different, we see at once that we cannot expect a simple connection between the frequency calculated by (1) of the radiation corresponding to a transition between two stationary states and the motions of the system in these states, except in the limit where  $n$  is very large, and where the ratio between the frequencies of the motion in successive stationary states differs very little from unity. Consider now a transition between the state corresponding to  $n = n'$  and the state corresponding to  $n = n''$ , and let us assume that  $n'$  and  $n''$  are large numbers and that  $n' - n''$  is small compared with  $n'$  and  $n''$ . In that case we may in (8) for  $\partial E$  put  $E' - E''$  and for  $\partial I$  put  $I' - I''$ , and we get therefore from (1) and (10) for the frequency of the radiation emitted or absorbed during the transition between the two states

$$\nu = \frac{1}{h} (E' - E'') = \frac{\omega}{h} (I' - I'') = (n' - n'') \omega. \quad (13)$$

Now in a stationary state of a periodic system the displacement of the particles in any given direction may always be expressed by means of a FOURIER-series as a sum of harmonic vibrations:

$$\xi = \sum C_\tau \cos 2\pi(\tau\omega t + c_\tau), \quad (14)$$

where the  $C$ 's and  $c$ 's are constants and the summation is to be extended over all positive entire values of  $\tau$ . On the ordinary theory of radiation we should therefore expect the system to emit a spectrum consisting of a series of lines of frequencies equal to  $\tau\omega$ , but, as it is seen, this is just equal to the series of frequencies which we obtain from (13) by introducing different values for  $n' - n''$ . As far as the frequencies are concerned we see therefore that in the limit where  $n$  is large there exists a close relation between the ordinary theory of radiation and the theory of spectra based on (1) and (10). It may be noticed, however, that, while on the first theory radiations of the different frequencies  $\tau\omega$  corresponding to different values of  $\tau$  are emitted or absorbed at the same time, these frequencies will on the present theory, based on the fundamental assumption I and II, be connected with entirely different processes of emission or absorption, corresponding to the transition of the system from a given state to different neighbouring stationary states.

In order to obtain the necessary connection, mentioned in the former section, to the ordinary theory of radiation in the limit of slow vibrations, we must further claim that a relation, as that just proved for the frequencies, will, in the limit of large  $n$ , hold also for the intensities of the different lines in the spectrum. Since now on ordinary electrodynamics the intensities of the radiations corresponding to different values of  $\tau$  are directly determined from the coefficients  $C_\tau$  in (14), we must therefore expect that for large values of  $n$  these coefficients will on the quantum theory determine the probability of spontaneous transition from a given stationary state for which  $n = n'$  to a neighbouring state for which  $n = n'' = n' - \tau$ . Now, this connection between the amplitudes of the different harmonic vibrations into



which the motion can be resolved, characterised by different values of  $\tau$ , and the probabilities of transition from a given stationary state to the different neighbouring stationary states, characterised by different values of  $n' - n''$ , may clearly be expected to be of a general nature. Although, of course, we cannot without a detailed theory of the mechanism of transition obtain an exact calculation of the latter probabilities, unless  $n$  is large, we may expect that also for small values of  $n$  the amplitude of the harmonic vibrations corresponding to a given value of  $\tau$  will in some way give a measure for the probability of a transition between two states for which  $n' - n''$  is equal to  $\tau$ . Thus in general there will be a certain probability of an atomic system in a stationary state to pass spontaneously to any other state of smaller energy, but if for all motions of a given system the coefficients  $C$  in (14) are zero for certain values of  $\tau$ , we are led to expect that no transition will be possible, for which  $n' - n''$  is equal to one of these values.

A simple illustration of these considerations is offered by the linear harmonic vibrator mentioned above in connection with PLANCK's theory. Since in this case  $C_\tau$  is equal to zero for any  $\tau$  different from 1, we shall expect that for this system only such transitions are possible in which  $n$  alters by one unit. From (1) and (9) we obtain therefore the simple result that the frequency of any radiation emitted or absorbed by a linear harmonic vibrator is equal to the constant frequency  $\omega_0$ . This result seems to be supported by observations on the absorption-spectra of diatomic gases, showing that certain strong absorption-lines, which according to general evidence may be ascribed to vibrations of the two atoms in the molecule relative to each other, are not accompanied by lines of the same order of intensity and corresponding to entire multipla of the frequency, such as it should be expected from (1) if the system had any considerable tendency to pass between non-successive states. In this connection it may be noted that the fact, that in the absorption spectra of some diatomic gases faint lines occur corresponding to the double frequency of the main lines,<sup>1)</sup> obtains a natural explanation by assuming that for finite amplitudes the vibrations are not exactly harmonic and that therefore the molecules possess a small probability of passing also between non-successive states.

### § 3. Conditionally periodic systems.

If we consider systems of several degrees of freedom the motion will be periodic only in singular cases and the general conditions which determine the stationary states cannot therefore be derived by means of the same simple kind of considerations as in the former section. As mentioned in the introduction, however, SOMMERFELD and others have recently succeeded, by means of a suitable generalisation of (10), to obtain conditions for an important class of systems of several degrees of freedom,

<sup>1)</sup> See E. C. KEMBLE, *Phys. Rev.*, VIII, p. 701, 1916.



which, in connection with (1), have been found to give results in convincing agreement with experimental results about line-spectra. Subsequently these conditions have been proved by EHRENFEST and especially by BURGERS<sup>1)</sup> to be invariant for slow mechanical transformations.

To the generalisation under consideration we are naturally led, if we first consider such systems for which the motions corresponding to the different degrees of freedom are dynamically independent of each other. This occurs if the expression for the total energy  $E$  in HAMILTONS equations (4) for a system of  $s$  degrees of freedom can be written as a sum  $E_1 + \dots + E_s$ , where  $E_k$  contains  $q_k$  and  $p_k$  only. An illustration of a system of this kind is presented by a particle moving in a field of force in which the force-components normal to three mutually perpendicular fixed planes are functions of the distances from these planes respectively. Since in such a case the motion corresponding to each degree of freedom in general will be periodic, just as for a system of one degree of freedom, we may obviously expect that the condition (10) is here replaced by a set of  $s$  conditions:

$$I_k = \int p_k dq_k = n_k h, \quad (k = 1, \dots, s) \quad (15)$$

where the integrals are taken over a complete period of the different  $q$ 's respectively, and where  $n_1, \dots, n_s$  are entire numbers. It will be seen at once that these conditions are invariant for any slow transformation of the system for which the independency of the motions corresponding to the different coordinates is maintained.

A more general class of systems for which a similar analogy with systems of a single degree of freedom exists and where conditions of the same type as (15) present themselves is obtained in the case where, although the motions corresponding to the different degrees of freedom are not independent of each other, it is possible nevertheless by a suitable choice of coordinates to express each of the momenta  $p_k$  as a function of  $q_k$  only. A simple system of this kind consists of a particle moving in a plane orbit in a central field of force. Taking the length of the radius-vector from the centre of the field to the particle as  $q_1$ , and the angular distance of this radius-vector from a fixed line in the plane of the orbit as  $q_2$ , we get at once from (4), since  $E$  does not contain  $q_2$ , the well known result that during the motion the angular momentum  $p_2$  is constant and that the radial motion, given by the variations of  $p_1$  and  $q_1$  with the time, will be exactly the same as for a system of one degree of freedom. In his fundamental application of the quantum theory to the spectrum of a non-periodic system SOMMERFELD assumed, therefore that the stationary states of the above system are given by two conditions of the form:

$$I_1 = \int p_1 dq_1 = n_1 h, \quad I_2 = \int p_2 dq_2 = n_2 h. \quad (16)$$

<sup>1)</sup> J. M. BURGERS, Versl. Akad. Amsterdam, XXV, pp. 849, 918, 1055 (1917), Ann. d. Phys. LII. p. 195 (1917), Phil. Mag. XXXIII, p. 514 (1917).

While the first integral obviously must be taken over a period of the radial motion, there might at first sight seem to be a difficulty in fixing the limits of integration of  $q_2$ . This disappears, however, if we notice that an integral of the type under consideration will not be altered by a change of coordinates in which  $q$  is replaced by some function of this variable. In fact, if instead of the angular distance of the radius-vector we take for  $q_2$  some continuous periodic function of this angle with period  $2\pi$ , every point in the plane of the orbit will correspond to one set of coordinates only and the relation between  $p$  and  $q$  will be exactly of the same type as for a periodic system of one degree of freedom for which the motion is of oscillating type. It follows therefore that the integration in the second of the conditions (16) has to be taken over a complete revolution of the radius-vector, and that consequently this condition is equivalent with the simple condition that the angular momentum of the particle round the centre of the field is equal to an entire multiplicity of  $\frac{h}{2\pi}$ . As pointed out by EHRENFEST, the conditions (16) are invariant for such special transformations of the system for which the central symmetry is maintained. This follows immediately from the fact that the angular momentum in transformations of this type remains invariant, and that the equations of motion for the radial coordinate as long as  $p_2$  remains constant are the same as for a system of one degree of freedom. On the basis of (16), SOMMERFELD has, as mentioned in the introduction, obtained a brilliant explanation of the fine structure of the lines in the hydrogen spectrum, due to the change of the mass of the electron with its velocity.<sup>1)</sup> To this theory we shall come back in Part II.

As pointed out by EPSTEIN<sup>2)</sup> and SCHWARZSCHILD<sup>3)</sup> the central systems considered by SOMMERFELD form a special case of a more general class of systems for which conditions of the same type as (15) may be applied. These are the so-called conditionally periodic systems, to which we are led if the equations of motion are discussed by means of the HAMILTON-JACOBI partial differential equation<sup>4)</sup>. In the expression for the total energy  $E$  as a function of the  $q$ 's and the  $p$ 's, let the latter quantities be replaced by the partial differential coefficients of some function

<sup>1)</sup> In this connection it may be remarked that conditions of the same type as (16) were proposed independently by W. WILSON (Phil. Mag. XXIX p. 795 (1915) and XXXI p. 156 (1916)), but by him applied only to the simple Keplerian motion described by the electron in the hydrogen atom if the relativity modifications are neglected. Due to the singular position of periodic systems in the quantum theory of systems of several degrees of freedom this application, however, involves, as it will appear from the following discussion, an ambiguity which deprives the result of an immediate physical interpretation. Conditions analogous to (16) have also been established by PLANCK in his interesting theory of the "physical structure of the phase space" of systems of several degrees of freedom (Verh. d. D. Phys. Ges. XVII p. 407 and p. 438 (1915), Ann. d. Phys. L p. 385, 1916). This theory, which has no direct relation to the problem of line-spectra discussed in the present paper, rests upon a profound analysis of the geometrical problem of dividing the multiple-dimensional phase space corresponding to a system of several degrees of freedom into "cells" in a way analogous to the division of the phase surface of a system of one degree of freedom by the curves given by (10).

<sup>2)</sup> P. EPSTEIN, loc. cit.

<sup>3)</sup> K. SCHWARZSCHILD, loc. cit.

<sup>4)</sup> See f. inst. C. V. L. CHARLIER, Die Mechanik des Himmels. Bd. I, Abt. 2.

$S$  with respect to the corresponding  $q$ 's respectively, and consider the partial differential equation:

$$E\left(q_1, \dots, q_s, \frac{\partial S}{\partial q_1}, \dots, \frac{\partial S}{\partial q_s}\right) = a_1, \quad (17)$$

obtained by putting this expression equal to an arbitrary constant  $a_1$ . If then

$$S = F(q_1, \dots, q_s, a_1, \dots, a_s) + C,$$

where  $a_2, \dots, a_s$  and  $C$  are arbitrary constants like  $a_1$ , is a total integral of (17), we get, as shown by HAMILTON and JACOBI, the general solution of the equations of motion (4) by putting

$$\frac{\partial S}{\partial a_1} = t + \beta_1, \quad \frac{\partial S}{\partial a_k} = \beta_k, \quad (k = 2, \dots, s) \quad (18)$$

and

$$\frac{\partial S}{\partial q_k} = p_k, \quad (k = 1, \dots, s) \quad (19)$$

where  $t$  is the time and  $\beta_1, \dots, \beta_s$  a new set of arbitrary constants. By means of (18) the  $q$ 's are given as functions of the time  $t$  and the  $2s$  constants  $a_1, \dots, a_s, \beta_1, \dots, \beta_s$  which may be determined for instance from the values of the  $q$ 's and  $\dot{q}$ 's at a given moment.

Now the class of systems, referred to, is that for which, for a suitable choice of orthogonal coordinates, it is possible to find a total integral of (17) of the form

$$S = \sum_1^s S_k(q_k, a_1, \dots, a_s), \quad (20)$$

where  $S_k$  is a function of the  $s$  constants  $a_1, \dots, a_s$  and of  $q_k$  only. In this case, in which the equation (17) allows of what is called "separation of variables", we get from (19) that every  $p$  is a function of the  $a$ 's and of the corresponding  $q$  only. If during the motion the coordinates do not become infinite in the course of time or converge to fixed limits, every  $q$  will, just as for systems of one degree of freedom, oscillate between two fixed values, different for the different  $q$ 's and depending on the  $a$ 's. Like in the case of a system of one degree of freedom,  $p_k$  will become zero and change its sign whenever  $q_k$  passes through one of these limits. Apart from special cases, the system will during the motion never pass twice through a configuration corresponding to the same set of values for the  $q$ 's and  $p$ 's, but it will in the course of time pass within any given, however small, distance from any configuration corresponding to a given set of values  $q_1, \dots, q_s$ , representing a point within a certain closed  $s$ -dimensional extension limited by  $s$  pairs of  $(s-1)$ -dimensional surfaces corresponding to constant values of the  $q$ 's equal to the above mentioned limits of oscillation. A motion of this kind is called "conditionally periodic". It will be seen that the character of the motion will depend only on the  $a$ 's and not on the  $\beta$ 's, which latter constants serve only to fix the exact configuration of the



system at a given moment, when the  $\alpha$ 's are known. For special systems it may occur that the orbit will not cover the above mentioned  $s$ -dimensional extension everywhere dense, but will, for all values of the  $\alpha$ 's, be confined to an extension of less dimensions. Such a case we will refer to in the following as a case of "degeneration".

Since for a conditionally periodic system which allows of separation in the variables  $q_1, \dots, q_s$  the  $p$ 's are functions of the corresponding  $q$ 's only, we may, just as in the case of independent degrees of freedom or in the case of quasi-periodic motion in a central field, form a set of expressions of the type

$$I_k = \int p_k(q_k, a_1, \dots, a_s) dq_k, \quad (k = 1, \dots, s) \quad (21)$$

where the integration is taken over a complete oscillation of  $q_k$ . As, in general, the orbit will cover everywhere dense an  $s$ -dimensional extension limited in the characteristic way mentioned above, it follows that, except in cases of degeneration, a separation of variables will not be possible for two different sets of coordinates  $q_1, \dots, q_s$  and  $q'_1, \dots, q'_s$ , unless  $q_1 = f_1(q'_1), \dots, q_s = f_s(q'_s)$ , and since a change of coordinates of this type will not affect the values of the expressions (21), it will be seen that the values of the  $I$ 's are completely determined for a given motion of the system. By putting

$$I_k = n_k h, \quad (k = 1, \dots, s) \quad (22)$$

where  $n_1, \dots, n_s$  are positive entire numbers, we obtain therefore a set of conditions which form a natural generalisation of condition (10) holding for a system of one degree of freedom.

Since the  $I$ 's, as given by (21), depend on the constants  $a_1, \dots, a_s$  only and not on the  $\beta$ 's, the  $\alpha$ 's may, in general, inversely be determined from the values of the  $I$ 's. The character of the motion will therefore, in general, be completely determined by the conditions (22), and especially the value for the total energy, which according to (17) is equal to  $\alpha_1$ , will be fixed by them. In the cases of degeneration referred to above, however, the conditions (22) involve an ambiguity, since in general for such systems there will exist an infinite number of different sets of coordinates which allow of a separation of variables, and which will lead to different motions in the stationary states, when these conditions are applied. As we shall see below, this ambiguity will not influence the fixation of the total energy in the stationary states, which is the essential factor in the theory of spectra based on (1) and in the applications of the quantum theory to statistical problems.

A well known characteristic example of a conditionally periodic system is afforded by a particle moving under the influence of the attractions from two fixed centres varying as the inverse squares of the distances apart, if the relativity modifications are neglected. As shown by JACOBI this problem can be solved by a separation of variables if so called elliptical coordinates are used, i. e. if for  $q_1$  and  $q_2$  we take two parameters characterising respectively an ellipsoid and a hyperboloid of revolution with the centres as foci and passing through the instantaneous posi-



tion of the moving particle, and for  $q_3$  we take the angle between the plane through the particle and the centres and a fixed plane through the latter points, or, in closer conformity with the above general description, some continuous periodic function of this angle with period  $2\pi$ . A limiting case of this problem is afforded by an electron rotating round a positive nucleus and subject to the effect of an additional homogeneous electric field, because this field may be considered as arising from a second nucleus at infinite distance apart from the first. The motion in this case will therefore be conditionally periodic and allow a separation of variables in parabolic coordinates, if the nucleus is taken as focus for both sets of paraboloids of revolution, and their axes are taken parallel to the direction of the electric force. By applying the conditions (22) to this motion EPSTEIN and SCHWARZSCHILD have, as mentioned in the introduction, independent of each other, obtained an explanation of the effect of an external electric field on the lines of the hydrogen spectrum, which was found to be in convincing agreement with STARK's measurements. To the results of these calculations we shall return in Part II.

In the above way of representing the general theory we have followed the same procedure as used by EPSTEIN. By introducing the so called "angle-variables" well known from the astronomical theory of perturbations, SCHWARZSCHILD has given the theory a very elegant form in which the analogy with systems of one degree of freedom presents itself in a somewhat different manner. The connection between this treatment and that given above has been discussed in detail by EPSTEIN.<sup>1)</sup>

As mentioned above the conditions (22), first established from analogy with systems of one degree of freedom, have subsequently been proved generally to be mechanically invariant for any slow transformation for which the system remains conditionally periodic. The proof of this invariance has been given quite recently by BURGERS<sup>2)</sup> by means of an interesting application of the theory of contact-transformations based on SCHWARZSCHILD's introduction of angle variables. We shall not enter here on these calculations but shall only consider some points in connection with the problem of the mechanical transformability of the stationary states which are of importance for the logical consistency of the general theory and for the later applications. In § 2 we saw that in the proof of the mechanical invariance of relation (10) for a periodic system of one degree of freedom, it was essential that the comparative variation of the external conditions during the time of one period could be made small. This may be regarded as an immediate consequence of the nature of the fixation of the stationary states in the quantum theory. In fact the answer to the question, whether a given state of a system is stationary, will not depend only on the motion of the particles at a given moment or on the field of force in the immediate neighbourhood of their instantaneous positions, but cannot be given before the particles have passed through a complete cycle of states, and so to speak

<sup>1)</sup> P. EPSTEIN, *Ann. d. Phys.* LI, p. 168 (1916). See also Note on page 29 of the present paper.

<sup>2)</sup> J. M. BURGERS, *loc. cit.* Versl. Akad. Amsterdam, XXV, p. 1055 (1917).

have got to know the entire field of force of influence on the motion. If thus, in the case of a periodic system of one degree of freedom, the field of force is varied by a given amount, and if its comparative variation within the time of a single period was not small, the particle would obviously have no means to get to know the nature of the variation of the field and to adjust its stationary motion to it, before the new field was already established. For exactly the same reasons it is a necessary condition for the mechanical invariance of the stationary states of a conditionally periodic system, that the alteration of the external conditions during an interval in which the system has passed approximately through all possible configurations within the above mentioned  $s$ -dimensional extension in the coordinate-space can be made as small as we like. This condition forms therefore also an essential point in BURGERS' proof of the invariance of the conditions (22) for mechanical transformations. Due to this we meet with a characteristic difficulty when during the transformation of the system we pass one of the cases of degeneration mentioned above, where, for every set of values for the  $a$ 's, the orbit will not cover the  $s$ -dimensional extension everywhere dense, but will be confined to an extension of less dimensions. It is clear that, when by a slow transformation of a conditionally periodic system we approach a degenerate system of this kind, the time-interval which the orbit takes to pass close to any possible configuration will tend to be very long and will become infinite when the degenerate system is reached. As a consequence of this the conditions (22) will generally not remain mechanically invariant when we pass a degenerate system, what has intimate connection with the above mentioned ambiguity in the determination of the stationary states of such systems by means of (22).

A typical case of a degenerate system, which may serve as an illustration of this point, is formed by a system of several degrees of freedom for which every motion is simply periodic, independent of the initial conditions. In this case, which is of great importance in the physical applications, we have from (5) and (21), for any set of coordinates in which a separation of variables is possible,

$$I = \int_0^\sigma (p_1 \dot{q}_1 + \dots + p_s \dot{q}_s) dt = x_1 I_1 + \dots + x_s I_s, \quad (23)$$

where the integration is extended over one period of the motion, and where  $x_1, \dots, x_s$  are a set of positive entire numbers without a common divisor. Now we shall expect that every motion, for which it is possible to find a set of coordinates in which it satisfies (22), will be stationary. For any such motion we get from (23)

$$I = (x_1 n_1 + \dots + x_s n_s) h = n h, \quad (24)$$

where  $n$  is a whole number which may take all positive values if, as in the applications mentioned below, at least one of the  $x$ 's is equal to one. Inversely, if the system under consideration allows of separation of variables in an infinite continuous multitude of sets of coordinates, we must conclude that generally every

motion which satisfies (24) will be stationary, because in general it will be possible for any such motion to find a set of coordinates in which it satisfies also (22). It will thus be seen that, for a periodic system of several degrees of freedom, condition (24) forms a simple generalisation of condition (10). From relation (8), which holds for two neighbouring motions of any periodic system, it follows further that the energy of the system will be completely determined by the value of  $I$ , just as for systems of one degree of freedom.

Consider now a periodic system in some stationary state satisfying (24), and let us assume that an external field is slowly established at a continuous rate and that the motion at any moment during this process allows of a separation of variables in a certain set of coordinates. If we would assume that the effect of the field on the motion of the system at any moment could be calculated directly by means of ordinary mechanics, we would find that the values of the  $I$ 's with respect to the latter coordinates would remain constant during the process, but this would involve that the values of the  $n$ 's in (22) would in general not be entire numbers, but would depend entirely on the accidental motion, satisfying (24), originally possessed by the system. That mechanics, however, cannot generally be applied directly to determine the motion of a periodic system under influence of an increasing external field, is just what we should expect according to the singular position of degenerate systems as regards mechanical transformations. In fact, in the presence of a small external field, the motion of a periodic system will undergo slow variations as regards the shape and position of the orbit, and if the perturbed motion is conditionally periodic these variations will be of a periodic nature. Formally, we may therefore compare a periodic system exposed to an external field with a simple mechanical system of one degree of freedom in which the particle performs a slow oscillating motion. Now the frequency of a slow variation of the orbit will be seen to be proportional to the intensity of the external field, and it is therefore obviously impossible to establish the external field at a rate so slow that the comparative change of its intensity during a period of this variation is small. The process which takes place during the increase of the field will thus be analogous to that which takes place if an oscillating particle is subject to the effect of external forces which change considerably during a period. Just as the latter process generally will give rise to emission or absorption of radiation and cannot be described by means of ordinary mechanics, we must expect that the motion of a periodic system of several degrees of freedom under the establishment of the external field cannot be determined by ordinary mechanics, but that the field will give rise to effects of the same kind as those which occur during a transition between two stationary states accompanied by emission or absorption of radiation. Consequently we shall expect that, during the establishment of the field, the system will in general adjust itself in some unmechanical way until a stationary state is reached in which the frequency (or frequencies) of the above mentioned slow variation of the orbit has a relation to the additional energy of the system due to the presence of the external



field, which is of the same kind as the relation, expressed by (8) and (10), between the energy and frequency of a periodic system of one degree of freedom. As it will be shown in Part II in connection with the physical applications, this condition is just secured if the stationary states in the presence of the field are determined by the conditions (22), and it will be seen that these considerations offer a means of fixing the stationary states of a perturbed periodic system also in cases where no separation of variables can be obtained.

In consequence of the singular position of the degenerate systems in the general theory of stationary states of conditionally periodic systems, we obtain a means of connecting mechanically two different stationary states of a given system through a continuous series of stationary states without passing through systems in which the forces are very small and the energies in all the stationary states tend to coincide (comp. page 9). In fact, if we consider a given conditionally periodic system which can be transformed in a continuous way into a system for which every orbit is periodic and for which every state satisfying (24) will also satisfy (22) for a suitable choice of coordinates, it is clear in the first place that it is possible to pass in a mechanical way through a continuous series of stationary states from a state corresponding to a given set of values of the  $n$ 's in (22) to any other such state for which  $x_1 n_1 + \dots + x_s n_s$  possesses the same value. If, moreover, there exists a second periodic system of the same character to which the first periodic system can be transformed continuously, but for which the set of  $x$ 's is different, it will be possible in general by a suitable cyclic transformation to pass in a mechanical way between any two stationary states of the given conditionally periodic system satisfying (22).

To obtain an example of such a cyclic transformation let us take the system consisting of an electron which moves round a fixed positive nucleus exerting an attraction varying as the inverse square of the distance. If we neglect the small relativity corrections, every orbit will be periodic independent of the initial conditions and the system will allow of separation of variables in polar coordinates as well as in any set of elliptical coordinates, of the kind mentioned on page 21, if the nucleus is taken as one of the foci. It is simply seen that any orbit which satisfies (24) for a value of  $n > 1$ , will also satisfy (22) for a suitable choice of elliptical coordinates. By imagining another nucleus of infinite small charge placed at the other focus, the orbit may further be transformed into another which satisfies (24) for the same value of  $n$ , but which may have any given value for the eccentricity. Consider now a state of the system satisfying (24), and let us assume that by the above means the orbit is originally so adjusted that in plane polar coordinates it will correspond to  $n_1 = m$  and  $n_2 = n - m$  in (16). Let then the system undergo a slow continuous transformation during which the field of force acting on the electron remains central, but by which the law of attraction is slowly varied until the force is directly proportional to the distance apart. In the final state, as well as in the original state, the orbit of the electron will be closed, but during the transformation the orbit will not be closed, and the ratio between the mean period of revolution and the period of the radial motion, which in the original motion was equal to one, will during the transformation increase continuously until in the final state it is equal to two. This means that, using polar coordinates, the values of  $x_1$  and  $x_2$  in (22) which for the first state are equal to  $x_1 = x_2 = 1$ , will be for the second state  $x_1 = 2$  and  $x_2 = 1$ . Since during the transformation  $n_1$  and  $n_2$  will keep their values, we get therefore in the final state  $I = h(2m + (n - m)) = h(n + m)$ . Now in the latter state, the system allows a separation of



variables not only in polar coordinates but also in any system of rectangular Cartesian coordinates, and by suitable choice of the direction of the axes, we can obtain that any orbit, satisfying (24) for a value of  $n > 1$ , will also satisfy (22). By an infinite small change of the force components in the directions of the axes, in such a way that the motions in these directions remain independent of each other but possess slightly different periods, it will further be possible to transform the elliptical orbit mechanically into one corresponding to any given ratio between the axes. Let us now assume that in this way the orbit of the electron is transformed into a circular one, so that, returning to plane polar coordinates, we have  $n_1 = 0$  and  $n_2 = n + m$ , and let then by a slow transformation the law of attraction be varied until again it is that of the inverse square. It will be seen that when this state is reached the motion will again satisfy (24), but this time we will have  $I = h(n + m)$  instead of  $I = nh$  as in the original state. By repeating a cyclic process of this kind we may pass from any stationary state of the system in question which satisfies (24) for a value of  $n > 1$  to any other such state without leaving at any moment the region of stationary states.

The theory of the mechanical transformability of the stationary states gives us a means to discuss the question of the a-priori probability of the different states of a conditionally periodic system, characterised by different sets of values for the  $n$ 's in (22). In fact from the considerations, mentioned in § 1, it follows that, if the a-priori probability of the stationary states of a given system is known, it is possible at once to deduce the probabilities for the stationary states of any other system to which the first system can be transformed continuously without passing through a system of degeneration. Now from the analogy with systems of one degree of freedom it seems necessary to assume that, for a system of several degrees of freedom for which the motions corresponding to the different coordinates are dynamically independent of each other, the a-priori probability is the same for all the states corresponding to different sets of  $n$ 's in (15). According to the above we shall therefore assume that the a-priori probability is the same for all states, given by (22), of any system which can be formed in a continuous way from a system of this kind without passing through systems of degeneration. It will be observed that on this assumption we obtain exactly the same relation to the ordinary theory of statistical mechanics in the limit of large  $n$ 's as obtained in the case of systems of one degree of freedom. Thus, for a conditionally periodic system, the volume given by (11) of the element of phase-space, including all points  $q_1, \dots, q_s, p_1, \dots, p_s$  which represent states for which the value of  $I_k$  given by (21) lies between  $I_k$  and  $I_k + \delta I_k$ , is seen at once to be equal to<sup>1)</sup>

$$\delta W = \delta I_1 \delta I_2 \dots \delta I_s, \quad (25)$$

if the coordinates are so chosen that the motion corresponding to every degree of freedom is of oscillating type. The volume of the phase-space limited by  $s$  pairs of surfaces, corresponding to successive values for the  $n$ 's in the conditions (22), will therefore be equal to  $h^s$  and consequently be the same for every combination of the  $n$ 's. In the limit where the  $n$ 's are large numbers and the stationary states

<sup>1)</sup> Comp. A. SOMMERFELD, Ber. Akad. München, 1917, p. 83.

corresponding to successive values for the  $n$ 's differ only very little from each other, we thus obtain the same result on the assumption of equal a-priori probability of all the stationary states, corresponding to different sets of values of  $n_1, n_2 \dots n_s$  in (22), as would be obtained by application of ordinary statistical mechanics.

The fact that the last considerations hold for every non-degenerate conditionally periodic system suggests the assumption that in general the a-priori probability will be the same for all the states determined by (22), even if it should not be possible to transform the given system into a system of independent degrees of freedom without passing through degenerate systems. This assumption will be shown to be supported by the consideration of the intensities of the different components of the STARK-effect of the hydrogen lines, mentioned in the next Part. When we consider a degenerate system, however, we cannot assume that the different stationary states are a-priori equally probable. In such a case the stationary states will be characterised by a number of conditions less than the number of degrees of freedom, and the probability of a given state must be determined from the number of different stationary states of some non-degenerate system which will coincide in the given state, if the latter system is continuously transformed into the degenerate system under consideration.

In order to illustrate this, let us take the simple case of a degenerate system formed by an electrified particle moving in a plane orbit in a central field, the stationary states of which are given by the two conditions (16). In this case the plane of the orbit is undetermined, and it follows already from a comparison with ordinary statistical mechanics, that the a-priori probability of the states characterized by different combinations of  $n_1$  and  $n_2$  in (16) cannot be the same. Thus the volume of the phase-space, corresponding to states for which  $I_1$  lies between  $I_1$  and  $I_1 + \delta I_1$  and for which  $I_2$  lies between  $I_2$  and  $I_2 + \delta I_2$ , is found by a simple calculation<sup>1)</sup> to be equal to  $\delta W = 2I_2 \delta I_1 \delta I_2$ , if the motion is described by ordinary polar coordinates. For large values of  $n_1$  and  $n_2$ , we must therefore expect that the a-priori probability of a stationary state corresponding to a given combination  $(n_1, n_2)$  is proportional to  $n_2$ . The question of the a-priori probability of states corresponding to small values of the  $n$ 's has been discussed by SOMMERFELD in connection with the problem of the intensities of the different components in the fine structure of the hydrogen lines (see Part II). From considerations about the volume of the extensions in the phase-space, which might be considered as associated with the states characterised by different combinations  $(n_1, n_2)$ , SOMMERFELD proposes several different expressions for the a-priori probability of such states. Due to the necessary arbitrariness involved in the choice of these extensions, however, we cannot in this way obtain a rational determination of the a-priori probability of states corresponding to small values of

<sup>1)</sup> See A. SOMMERFELD, loc. cit.

$n_1$  and  $n_2$ . On the other hand, this probability may be deduced by regarding the motion of the system under consideration as the degeneration of a motion characterised by three numbers  $n_1$ ,  $n_2$  and  $n_3$ , as in the general applications of the conditions (22) to a system of three degrees of freedom. Such a motion may be obtained for instance by imagining the system placed in a small homogeneous magnetic field. In certain respects this case falls outside the general theory of conditionally periodic systems discussed in this section, but, as we shall see in Part II, it can be simply shown that the presence of the magnetic field imposes the further condition on the motion in the stationary states that the angular momentum round the axis of the field is equal to  $n' \frac{h}{2\pi}$ , where  $n'$  is a positive entire number equal to or less than  $n_2$ , and which for the system considered in the spectral problems must be assumed to be different from zero. When regard is taken to the two opposite directions in which the particle may rotate round the axis of the field, we see therefore that for this system a state corresponding to a given combination of  $n_1$  and  $n_2$  in the presence of the field can be established in  $2n_2$  different ways. The a-priori probability of the different states of the system may consequently for all combinations of  $n_1$  and  $n_2$  be assumed to be proportional to  $n_2$ .

The assumption just mentioned that the angular momentum round the axis of the field cannot be equal to zero is deduced from considerations of systems for which the motion corresponding to special combinations of the  $n$ 's in (22) would become physically impossible due to some singularity in its character. In such cases we must assume that no stationary states exist corresponding to the combinations  $(n_1, n_2, \dots n_s)$  under consideration, and on the above principle of the invariance of the a-priori probability for continuous transformations we shall accordingly expect that the a-priori probability of any other state, which can be transformed continuously into one of these states without passing through cases of degeneration, will also be equal to zero.

Let us now proceed to consider the spectrum of a conditionally periodic system, calculated from the values of the energy in the stationary states by means of relation (1). If  $E(n_1, \dots n_s)$  is the total energy of a stationary state determined by (22) and if  $\nu$  is the frequency of the line corresponding to the transition between two stationary states characterised by  $n_k = n'_k$  and  $n_k = n''_k$  respectively, we have

$$\nu = \frac{1}{h} [E(n'_1, \dots n'_s) - E(n''_1, \dots n''_s)]. \quad (26)$$

In general, this spectrum will be entirely different from the spectrum to be expected on the ordinary theory of electrodynamics from the motion of the system. Just as for a system of one degree of freedom we shall see, however, that in the limit where the motions in neighbouring stationary states differ very little from each other, there exists a close relation between the spectrum calculated on the quantum theory and that to be expected on ordinary electrodynamics. As in § 2



we shall further see, that this connection leads to certain general considerations about the probability of transition between any two stationary states and about the nature of the accompanying radiation, which are found to be supported by observations. In order to discuss this question we shall first deduce a general expression for the energy difference between two neighbouring states of a conditionally periodic system, which can be simply obtained by a calculation analogous to that used in § 2 in the deduction of the relation (8).

Consider some motion of a conditionally periodic system which allows of separation of variables in a certain set of coordinates  $q_1, \dots, q_s$ , and let us assume that at the time  $t = \vartheta$  the configuration of the system will to a close approximation be the same as at the time  $t = 0$ . By taking  $\vartheta$  large enough we can make this approximation as close as we like. If next we consider some conditionally periodic motion, obtained by a small variation of the first motion, and which allows of separation of variables in a set of coordinates  $q'_1, \dots, q'_s$  which may differ slightly from the set  $q_1, \dots, q_s$ , we get by means of HAMILTON'S equations (4), using the coordinates  $q'_1, \dots, q'_s$ ,

$$\int_0^\vartheta \delta E dt = \int_0^\vartheta \sum_1^s \left( \frac{\partial E}{\partial p'_k} \delta p'_k + \frac{\partial E}{\partial q'_k} \delta q'_k \right) dt = \int_0^\vartheta \sum_1^s (\dot{q}'_k \delta p'_k - \dot{p}'_k \delta q'_k) dt.$$

By partial integration of the second term in the bracket this gives:

$$\int_0^\vartheta \delta E dt = \int_0^\vartheta \sum_1^s \delta (p'_k \dot{q}'_k) dt - \left[ \sum_1^s p'_k \delta q'_k \right]_{t=0}^{t=\vartheta} \quad (27)$$

Now we have for the unvaried motion

$$\int_0^\vartheta \sum_1^s p'_k \dot{q}'_k dt = \int_0^\vartheta \sum_1^s p_k \dot{q}_k dt = \sum_1^s N_k I_k,$$

where  $I_k$  is defined by (21) and where  $N_k$  is the number of oscillations performed by  $q_k$  in the time interval  $\vartheta$ . For the varied motion we have on the other hand:

$$\int_0^\vartheta \sum_1^s p'_k \dot{q}'_k dt = \int_{t=0}^{t=\vartheta} \sum_1^s p'_k dq'_k = \sum_1^s N_k I_k + \left[ \sum_1^s p'_k \delta q'_k \right]_{t=0}^{t=\vartheta},$$

where the  $I$ 's correspond to the conditionally periodic motion in the coordinates  $q'_1, \dots, q'_s$ , and the  $\delta q$ 's which enter in the last term are the same as those in (27). Writing  $I'_k - I_k = \delta I_k$ , we get therefore from the latter equation

$$\int_0^\vartheta \delta E dt = \sum_1^s N_k \delta I_k. \quad (28)$$



In the special case where the varied motion is an undisturbed motion belonging to the same system as the unvaried motion we get, since  $\partial E$  will be constant,

$$\partial E = \sum_1^s \omega_k \partial I_k, \quad (29)$$

where  $\omega_k = \frac{N_k}{\vartheta}$  is the mean frequency of oscillation of  $q_k$  between its limits, taken over a long time interval of the same order of magnitude as  $\vartheta$ . This equation forms a simple generalisation of (8), and in the general case in which a separation of variables will be possible only for one system of coordinates leading to a complete definition of the  $I$ 's it might have been deduced directly from the analytical theory of the periodicity properties of the motion of a conditionally periodic system, based on the introduction of angle-variables.<sup>1)</sup> From (29) it follows more-

<sup>1)</sup> See CHARLIER, *Die Mechanik des Himmels*, Bd. I Abt. 2, and especially P. EPSTEIN, *Ann. d. Phys.* LI p. 178 (1916). By means of the well known theorem of JACOBI about the change of variables in the canonical equations of HAMILTON, the connection between the notion of angle-variables and the quantities  $I$ , discussed by EPSTEIN in the latter paper, may be briefly exposed in the following elegant manner which has been kindly pointed out to me by Mr. H. A. KRAMERS. Consider the function  $S(q_1, \dots, q_s, I_1, \dots, I_s)$  obtained from (20) by introducing for the  $\alpha$ 's their expressions in terms of the  $I$ 's given by the equations (21). This function will be a many valued function of the  $q$ 's which increases by  $I_k$  if  $q_k$  describes one oscillation between its limits and comes back to its original value while the other  $q$ 's remain constant. If we therefore introduce a new set of variables  $w_1, \dots, w_s$  defined by

$$w_k = \frac{\partial S}{\partial I_k}, \quad (k = 1, \dots, s) \quad (1^*)$$

it will be seen that  $w_k$  increases by one unit while the other  $w$ 's will come back to their original values if  $q_k$  describes one oscillation between its limits and the other  $q$ 's remain constant. Inversely it will therefore be seen that the  $q$ 's, and also the  $p$ 's which were given by

$$p_k = \frac{\partial S}{\partial q_k}, \quad (k = 1, \dots, s), \quad (2^*)$$

when considered as functions of the  $I$ 's and  $w$ 's will be periodic functions of every of the  $w$ 's with period 1. According to Fourier's theorem any of the  $q$ 's may therefore be represented by an  $s$ -double trigonometric series of the form

$$q = \sum A_{\tau_1, \dots, \tau_s} \cos 2\pi(\tau_1 w_1 + \dots + \tau_s w_s + \alpha_{\tau_1, \dots, \tau_s}), \quad (3^*)$$

where the  $A$ 's and  $\alpha$ 's are constants depending on the  $I$ 's and where the summation is to be extended over all entire values of  $\tau_1, \dots, \tau_s$ . On account of this property of the  $w$ 's, the quantities  $2\pi w_1, \dots, 2\pi w_s$  are denoted as "angle variables". Now from (1<sup>\*</sup>) and (2<sup>\*</sup>) it follows according to the above mentioned theorem of JACOBI (see for instance JACOBI, *Vorlesungen über Dynamik* § 37) that the variations with the time of the  $I$ 's and  $w$ 's will be given by

$$\frac{dI_k}{dt} = -\frac{\partial E}{\partial w_k}, \quad \frac{dw_k}{dt} = \frac{\partial E}{\partial I_k}, \quad (k = 1, \dots, s) \quad (4^*)$$

where the energy  $E$  is considered as a function of the  $I$ 's and  $w$ 's. Since  $E$ , however, is determined by the  $I$ 's only we get from (4<sup>\*</sup>), besides the evident result that the  $I$ 's are constant during the motion, that the  $w$ 's will vary linearly with the time and can be represented by

$$w_k = \omega_k t + \delta_k, \quad \omega_k = \frac{\partial E}{\partial I_k}, \quad (k = 1, \dots, s) \quad (5^*)$$

where  $\delta_k$  is a constant, and where  $\omega_k$  is easily seen to be equal to the mean frequency of oscillation

over that, if the system allows of a separation of variables in an infinite continuous multitude of sets of coordinates, the total energy will be the same for all motions corresponding to the same values of the  $I$ 's, independent of the special set of coordinates used to calculate these quantities. As mentioned above and as we have already shown in the case of purely periodic systems by means of (8), the total energy is therefore also in cases of degeneration completely determined by the conditions (22).

Consider now a transition between two stationary states determined by (22) by putting  $n_k = n'_k$  and  $n_k = n''_k$  respectively, and let us assume that  $n'_1, \dots, n'_s, n''_1, \dots, n''_s$  are large numbers, and that the differences  $n'_k - n''_k$  are small compared with these numbers. Since the motions of the system in these states will differ relatively very little from each other we may calculate the difference of the energy by means of (29), and we get therefore, by means of (1), for the frequency of the radiation corresponding to the transition between the two states

$$\nu = \frac{1}{h}(E' - E'') = \frac{1}{h} \sum_1^s \omega_k (I'_k - I''_k) = \sum_1^s \omega_k (n'_k - n''_k), \quad (30)$$

which is seen to be a direct generalisation of the expression (13) in § 2.

Now, in complete analogy to what is the case for periodic systems of one degree of freedom, it is proved in the analytical theory of the motion of conditionally periodic systems mentioned above that for the latter systems the coordinates  $q_1, \dots, q_s$ , and consequently also the displacements of the particles in any given direction, may be expressed as a function of the time by an  $s$ -double infinite FOURIER series of the form:

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of  $q_k$ . From (5\*) equation (28) follows at once, and it will further be seen that by introducing (5\*) in (3\*) we get the result that every of the  $q$ 's, and consequently also any one-valued function of the  $q$ 's, can be represented by an expression of the type (31).

In this connection it may be mentioned that the method of SCHWARZSCHILD of fixing the stationary states of a conditionally periodic system, mentioned on page 21, consists in seeking for a given system a set of canonically conjugated variables  $Q_1, \dots, Q_s, P_1, \dots, P_s$  in such a way that the positional coordinates of the system  $q_1, \dots, q_s$  and their conjugated momenta  $p_1, \dots, p_s$ , when considered as functions of the  $Q$ 's and  $P$ 's, are periodic in every of the  $Q$ 's with period  $2\pi$ , while the energy of the system depends only on the  $P$ 's. In analogy with the condition which fixes the angular momentum in SOMMERFELD's theory of central systems SCHWARZSCHILD next puts every of the  $P$ 's equal to an entire multiplum of  $\frac{h}{2\pi}$ . In contrast to the theory of stationary states of conditionally periodic systems based on the possibility of separation of variables and the fixation of the  $I$ 's by (22), this method does not lead to an absolute fixation of the stationary states, because, as pointed out by SCHWARZSCHILD himself, the above definition of the  $P$ 's leaves an arbitrary constant undetermined in every of these quantities. In many cases, however, these constants may be simply determined from considerations of mechanical transformability of the stationary states, and as pointed out by BURGERS (loc. cit. Versl. Akad. Amsterdam XXV p. 1055 (1917) SCHWARZSCHILD's method possesses on the other hand the essential advantage of being applicable to certain classes of systems in which the displacements of the particles may be represented by trigonometric series of the type (31), but for which the equations of motion cannot be solved by separation of variables in any fixed set of coordinates. An interesting application of this to the spectrum of rotating molecules, given by BURGERS, will be mentioned in Part IV.

$$\xi = \sum C_{\tau_1, \dots, \tau_s} \cos 2\pi \{ (\tau_1 \omega_1 + \dots + \tau_s \omega_s) t + c_{\tau_1, \dots, \tau_s} \}, \quad (31)$$

where the summation is to be extended over all positive and negative entire values of the  $\tau$ 's, and where the  $\omega$ 's are the above mentioned mean frequencies of oscillation for the different  $q$ 's. The constants  $C_{\tau_1, \dots, \tau_s}$  depend only on the  $\alpha$ 's in the equations (18) or, what is the same, on the  $I$ 's, while the constants  $c_{\tau_1, \dots, \tau_s}$  depend on the  $\alpha$ 's as well as on the  $\beta$ 's. In general the quantities  $\tau_1 \omega_1 + \dots + \tau_s \omega_s$  will be different for any two different sets of values for the  $\tau$ 's, and in the course of time the orbit will cover everywhere dense a certain  $s$ -dimensional extension. In a case of degeneration, however, where the orbit will be confined to an extension of less dimensions, there will exist for all values of the  $\alpha$ 's one or more relations of the type  $m_1 \omega_1 + \dots + m_s \omega_s = 0$  where the  $m$ 's are entire numbers and by the introduction of which the expression (31) can be reduced to a FOURIER series which is less than  $s$ -double infinite. Thus in the special case of a system of which every orbit is periodic we have  $\frac{\omega_1}{\kappa_1} = \dots = \frac{\omega_s}{\kappa_s} = \omega$ , where the  $\kappa$ 's are the numbers which enter in equation (23), and the FOURIER series for the displacements in the different directions will in this case consist only of terms of the simple form  $C_\tau \cos 2\pi \{ \tau \omega t + c_\tau \}$ , just as for a system of one degree of freedom.

On the ordinary theory of radiation, we should expect from (31) that the spectrum emitted by the system in a given state would consist of an  $s$ -double infinite series of lines of frequencies equal to  $\tau_1 \omega_1 + \dots + \tau_s \omega_s$ . In general, this spectrum would be completely different from that given by (26). This follows already from the fact that the  $\omega$ 's will depend on the values for the constants  $\alpha_1, \dots, \alpha_s$  and will vary in a continuous way for the continuous multitude of mechanically possible states corresponding to different sets of values for these constants. Thus in general the  $\omega$ 's will be quite different for two different stationary states corresponding to different sets of  $n$ 's in (22), and we cannot expect any close relation between the spectrum calculated on the quantum theory and that to be expected on the ordinary theory of mechanics and electrodynamics. In the limit, however, where the  $n$ 's in (22)<sub>0</sub> are large numbers, the ratio between the  $\omega$ 's for two stationary states, corresponding to  $n_k = n'_k$  and  $n_k = n''_k$  respectively, will tend to unity if the differences  $n'_k - n''_k$  are small compared with the  $n$ 's, and as seen from (30) the spectrum calculated by (1) and (22) will in this limit just tend to coincide with that to be expected on the ordinary theory of radiation from the motion of the system.

As far as the frequencies are concerned, we thus see that for conditionally periodic systems there exists a connection between the quantum theory and the ordinary theory of radiation of exactly the same character as that shown in § 2 to exist in the simple case of periodic systems of one degree of freedom. Now on ordinary electrodynamics the coefficients  $C_{\tau_1, \dots, \tau_s}$  in the expression (31) for the displacements of the particles in the different directions would in the well known way determine the intensity and polarisation of the emitted radiation of the corresponding frequency  $\tau_1 \omega_1 + \dots + \tau_s \omega_s$ . As for systems of one degree of freedom



we must therefore conclude that, in the limit of large values for the  $n$ 's, the probability of spontaneous transition between two stationary states of a conditionally periodic system, as well as the polarisation of the accompanying radiation, can be determined directly from the values of the coefficient  $C_{\tau_1, \dots, \tau_s}$  in (31) corresponding to a set of  $\tau$ 's given by  $\tau_k = n'_k - n''_k$ , if  $n'_1, \dots, n'_s$  and  $n''_1, \dots, n''_s$  are the numbers which characterise the two stationary states.

Without a detailed theory of the mechanism of transition between the stationary states we cannot, of course, in general obtain an exact determination of the probability of spontaneous transition between two such states, unless the  $n$ 's are large numbers. Just as in the case of systems of one degree of freedom, however, we are naturally led from the above considerations to assume that, also for values of the  $n$ 's which are not large, there must exist an intimate connection between the probability of a given transition and the values of the corresponding FOURIER coefficient in the expressions for the displacements of the particles in the two stationary states. This allows us at once to draw certain important conclusions. Thus, from the fact that in general negative as well as positive values for the  $\tau$ 's appear in (31), it follows that we must expect that in general not only such transitions will be possible in which all the  $n$ 's decrease, but that also transitions will be possible for which some of the  $n$ 's increase while others decrease. This conclusion, which is supported by observations on the fine structure of the hydrogen lines as well as on the STARK effect, is contrary to the suggestion, put forward by SOMMERFELD with reference to the essential positive character of the  $F$ 's, that every of the  $n$ 's must remain constant or decrease under a transition. Another direct consequence of the above considerations is obtained if we consider a system for which, for all values of the constants  $a_1, \dots, a_s$ , the coefficient  $C_{\tau_1, \dots, \tau_s}$  corresponding to a certain set  $\tau_1^0, \dots, \tau_s^0$  of values for the  $\tau$ 's is equal to zero in the expressions for the displacements of the particles in every direction. In this case we shall naturally expect that no transition will be possible for which the relation  $n'_k - n''_k = \tau_k^0$  is satisfied for every  $k$ . In the case where  $C_{\tau_1^0, \dots, \tau_s^0}$  is equal to zero in the expressions for the displacement in a certain direction only, we shall expect that all transitions, for which  $n'_k - n''_k = \tau_k^0$  for every  $k$ , will be accompanied by a radiation which is polarised in a plane perpendicular to this direction.

A simple illustration of the last considerations is afforded by the system mentioned in the beginning of this section, and which consists of a particle executing motions in three perpendicular directions which are independent of each other. In that case all the FOURIER coefficients in the expressions for the displacements in any direction will disappear if more than one of the  $\tau$ 's are different from zero. Consequently we must assume that only such transitions are possible for which only one of the  $n$ 's varies at the same time, and that the radiation corresponding to such a transition will be linearly polarised in the direction of the displacement of the corresponding coordinate. In the special case where the motions in the three directions are simply harmonic, we shall moreover conclude that none



of the  $n$ 's can vary by more than a single unit, in analogy with the considerations in the former section about a linear harmonic vibrator.

Another example which has more direct physical importance, since it includes all the special applications of the quantum theory to spectral problems mentioned in the introduction, is formed by a conditionally periodic system possessing an axis of symmetry. In all these applications a separation of variables is obtained in a set of three coordinates  $q_1$ ,  $q_2$  and  $q_3$ , of which the first two serve to fix the position of the particle in a plane through the axis of the system, while the last is equal to the angular distance between this plane and a fixed plane through the same axis. Due to the symmetry, the expression for the total energy in HAMILTON'S equations will not contain the angular distance  $q_3$  but only the angular momentum  $p_3$  round the axis. The latter quantity will consequently remain constant during the motion, and the variations of  $q_1$  and  $q_2$  will be exactly the same as in a conditionally periodic system of two degrees of freedom only. If the position of the particle is described in a set of cylindrical coordinates  $z$ ,  $\rho$ ,  $\vartheta$ , where  $z$  is the displacement in the direction of the axis,  $\rho$  the distance of the particle from this axis and  $\vartheta$  is equal to the angular distance  $q_3$ , we have therefore

$$\begin{aligned} z &= \sum C_{\tau_1, \tau_2} \cos 2\pi \{ (\tau_1 \omega_1 + \tau_2 \omega_2) t + c_{\tau_1, \tau_2} \} \\ \text{and} \\ \rho &= \sum C'_{\tau_1, \tau_2} \cos 2\pi \{ (\tau_1 \omega_1 + \tau_2 \omega_2) t + c'_{\tau_1, \tau_2} \}, \end{aligned} \quad (32)$$

where the summation is to be extended over all positive and negative entire values of  $\tau_1$  and  $\tau_2$ , and where  $\omega_1$  and  $\omega_2$  are the mean frequencies of oscillation of the coordinates  $q_1$  and  $q_2$ . For the rate of variation of  $\vartheta$  with the time we have further

$$\frac{d\vartheta}{dt} = \dot{q}_3 = \frac{\partial E}{\partial p_3} = f(q_1, q_2, p_1, p_2, p_3) = \pm \sum C''_{\tau_1, \tau_2} \cos 2\pi \{ (\tau_1 \omega_1 + \tau_2 \omega_2) t + c''_{\tau_1, \tau_2} \},$$

where the two signs correspond to a rotation of the particle in the direction of increasing and decreasing  $q_3$  respectively, and are introduced to separate the two types of symmetrical motions corresponding to these directions. This gives

$$\pm \vartheta = 2\pi \omega_3 t + \sum C'''_{\tau_1, \tau_2} \cos 2\pi \{ (\tau_1 \omega_1 + \tau_2 \omega_2) t + c'''_{\tau_1, \tau_2} \}, \quad (33)$$

where the positive constant  $\omega_3 = \frac{1}{2\pi} C''_{0,0}$  is the mean frequency of rotation round the axis of symmetry of the system. Considering now the displacement of the particle in rectangular coordinates  $x$ ,  $y$  and  $z$ , and taking as above the axis of symmetry as  $z$ -axis, we get from (32) and (33) after a simple contraction of terms

$$\begin{aligned} x &= \rho \cos \vartheta = \sum D_{\tau_1, \tau_2} \cos 2\pi \{ (\tau_1 \omega_1 + \tau_2 \omega_2 + \omega_3) t + d_{\tau_1, \tau_2} \} \\ \text{and} \\ y &= \rho \sin \vartheta = \pm \sum D_{\tau_1, \tau_2} \sin 2\pi \{ (\tau_1 \omega_1 + \tau_2 \omega_2 + \omega_3) t + d_{\tau_1, \tau_2} \}, \end{aligned} \quad (34)$$

where the  $D$ 's and  $d$ 's are new constants, and the summation is again to be extended over all positive and negative values of  $\tau_1$  and  $\tau_2$ .

From (32) and (34) we see that the motion in the present case may be considered as composed of a number of linear harmonic vibrations parallel to the axis of symmetry and of frequencies equal to the absolute values of  $(\tau_1\omega_1 + \tau_2\omega_2)$ , together with a number of circular harmonic motions round this axis of frequencies equal to the absolute values of  $(\tau_1\omega_1 + \tau_2\omega_2 + \omega_3)$  and possessing the same direction of rotation as that of the moving particle or the opposite if the latter expression is positive or negative respectively. According to ordinary electrodynamics the radiation from the system would therefore consist of a number of components of frequency  $|\tau_1\omega_1 + \tau_2\omega_2|$  polarised parallel to the axis of symmetry, and a number of components of frequencies  $|\tau_1\omega_1 + \tau_2\omega_2 + \omega_3|$  and of circular polarisation round this axis (when viewed in the direction of the axis). On the present theory we shall consequently expect that in this case only two kinds of transitions between the stationary states given by (22) will be possible. In both of these  $n_1$  and  $n_2$  may vary by an arbitrary number of units, but in the first kind of transition, which will give rise to a radiation polarised parallel to the axis of the system,  $n_3$  will remain unchanged, while in the second kind of transition  $n_3$  will decrease or increase by one unit and the emitted radiation will be circularly polarised round the axis in the same direction as or the opposite of that of the rotation of the particle respectively.

In the next Part we shall see that these conclusions are supported in an instructive manner by the experiments on the effects of electric and magnetic fields on the hydrogen spectrum. In connection with the discussion of the general theory, however, it may be of interest to show that the formal analogy between the ordinary theory of radiation and the theory based on (1) and (22), in case of systems possessing an axis of symmetry, can be traced not only with respect to frequency relations but also by considerations of conservation of angular momentum. For a conditionally periodic system possessing an axis of symmetry the angular momentum round this axis is, with the above choice of coordinates, according to (22) equal to  $\frac{I_3}{2\pi} = n_3 \frac{h}{2\pi}$ . If therefore, as assumed above for a transition corresponding to an emission of linearly polarised light,  $n_3$  is unaltered, it means that the angular momentum of the system remains unchanged, while if  $n_3$  alters by one unit, as assumed for a transition corresponding to an emission of circularly polarised light, the angular momentum will be altered by  $\frac{h}{2\pi}$ . Now it is easily seen that the ratio between this amount of angular momentum and the amount of energy  $h\nu$  emitted during the transition is just equal to the ratio between the amount of angular momentum and energy possessed by the radiation which according to ordinary electrodynamics would be emitted by an electron rotating in a circular orbit in a central field of force. In fact, if  $a$  is the radius of the orbit,  $\nu$  the frequency of revolution and  $F$  the force of reaction due to the electromagnetic field of the radiation, the amount of energy and of angular momentum round an axis through the centre of the field perpendicular to the plane of the orbit, lost

by the electron in unit of time as a consequence of the radiation, would be equal to  $2\pi\nu aF$  and  $aF$  respectively. Due to the principles of conservation of energy and of angular momentum holding in ordinary electrodynamics, we should therefore expect that the ratio between the energy and the angular momentum of the emitted radiation would be  $2\pi\nu$ ,<sup>1)</sup> but this is seen to be equal to the ratio between the energy  $h\nu$  and the angular momentum  $\frac{h}{2\pi}$  lost by the system considered above during a transition for which we have assumed that the radiation is circularly polarised. This agreement would seem not only to support the validity of the above considerations but also to offer a direct support, independent of the equations (22), of the assumption that, for an atomic system possessing an axis of symmetry, the total angular momentum round this axis is equal to an entire multiple of  $\frac{h}{2\pi}$ .

A further illustration of the above considerations of the relation between the quantum theory and the ordinary theory of radiation is obtained if we consider a conditionally periodic system subject to the influence of a small perturbing field of force. Let us assume that the original system allows of separation of variables in a certain set of coordinates  $q_1, \dots, q_s$ , so that the stationary states are determined by (22). From the necessary stability of the stationary states we must conclude that the perturbed system will possess a set of stationary states which only differ slightly from those of the original system. In general, however, it will not be possible for the perturbed system to obtain a separation of variables in any set of coordinates, but if the perturbing force is sufficiently small the perturbed motion will again be of conditionally periodic type and may be regarded as a superposition of a number of harmonic vibrations just as the original motion. The displacements of the particles in the stationary states of the perturbed system will therefore be given by an expression of the same type as (31) where the fundamental frequencies  $\omega_k$  and the amplitudes  $C_{\tau_1, \dots, \tau_s}$  may differ from those corresponding to the stationary states of the original system by small quantities proportional to the intensity of the perturbing forces. If now for the original motion the coefficients  $C_{\tau_1, \dots, \tau_s}$  corresponding to certain combinations of the  $\tau$ 's are equal to zero for all values of the constants  $a_1, \dots, a_s$ , these coefficients will therefore for the perturbed motion, in general, possess small values proportional to the perturbing forces. From the above considerations we shall therefore expect that, in addition to the main probabilities of such transitions between stationary states which are possible for the original system, there will for the perturbed system exist small probabilities of new transitions corresponding to the above mentioned combinations of the  $\tau$ 's. Consequently we shall expect that the effect of the perturbing field on the spectrum of the system will consist partly in a small displacement of the original lines partly in the appearance of new lines of small intensity.

A simple example of this is afforded by a system consisting of a particle moving in a plane and executing harmonic vibrations in two perpendicular directions with fre-

<sup>1)</sup> Comp. K. SCHAPOSCHNIKOW, Phys. Zeitschr. XV, p. 454 (1914).



quencies  $\omega_1$  and  $\omega_2$ . If the system is undisturbed all coefficients  $C_{\tau_1, \tau_2}$  will be zero, except  $C_{1,0}$  and  $C_{0,1}$ . When, however, the system is perturbed, for instance by an arbitrary small central force, there will in the FOURIER expressions for the displacements of the particle, in addition to the main terms corresponding to the fundamental frequencies  $\omega_1$  and  $\omega_2$ , appear a number of small terms corresponding to frequencies given by  $\tau_1 \omega_1 + \tau_2 \omega_2$  where  $\tau_1$  and  $\tau_2$  are entire numbers which may be positive as well as negative. On the present theory we shall therefore expect that in the presence of the perturbing force there will appear small probabilities for new transitions which will give rise to radiations analogous to the so-called harmonics and combination tones in acoustics, just as it should be expected on the ordinary theory of radiation where a direct connection between the emitted radiation and the motion of the system is assumed. Another example of more direct physical application is afforded by the effect of an external homogeneous electric field in producing new spectral lines. In this case the potential of the perturbing force is a linear function of the coordinates of the particles and, whatever is the nature of the original system, it follows directly from the general theory of perturbations that the frequency of any additional term in the expression for the perturbed motion, which is of the same order of magnitude as the external force, must correspond to the sum or difference of two frequencies of the harmonic vibrations into which the original motion can be resolved. With applications of these considerations we will meet in Part II in connection with the discussion of SOMMERFELD's theory of the fine structure of the hydrogen lines and in Part III in connection with the problem of the appearance of new series in the spectra of other elements under the influence of intense external electric fields.

As mentioned we cannot without a more detailed theory of the mechanism of transition between stationary states obtain quantitative information as regards the general question of the intensities of the different lines of the spectrum of a conditionally periodic system given by (26), except in the limit where the  $n$ 's are large numbers, or in such special cases where for all values of the constants  $a_1, \dots, a_s$  certain coefficients  $C_{\tau_1, \dots, \tau_s}$  in (31) are equal to zero. From considerations of analogy, however, we must expect that it will be possible also in the general case to obtain an estimate of the intensities of the different lines in the spectrum by comparing the intensity of a given line, corresponding to a transition between two stationary states characterised by the numbers  $n'_1, \dots, n'_s$  and  $n''_1, \dots, n''_s$  respectively, with the intensities of the radiations of frequencies  $\omega_1 (n'_1 - n''_1) + \dots + \omega_s (n'_s - n''_s)$  to be expected on ordinary electrodynamics from the motions in these states; although of course this estimate becomes more uncertain the smaller the values for the  $n$ 's are. As it will be seen from the applications mentioned in the following Parts this is supported in a general way by comparison with the observations.



## Part II.

### On the hydrogen spectrum.

#### § 1. The simple theory of the series spectrum of hydrogen.

As well known, the frequencies of the lines of the series spectrum of hydrogen may, if we look apart from the fine structure of the single lines revealed by instruments of high dispersive power, be represented by the formula

$$\nu = K \left( \frac{1}{n'^2} - \frac{1}{n''^2} \right), \quad (35)$$

where  $K$  is a constant, and  $n'$  and  $n''$  a set of two entire numbers, different for the different lines of the spectrum. According to the general principles of the quantum theory of line spectra discussed in the first section of Part I, we shall therefore expect that this spectrum is emitted by a system which possesses a series of stationary states in which the numerical value of the energy in the  $n^{\text{th}}$  state, omitting an arbitrary constant, with a high degree of approximation is given by

$$|E_n| = \frac{Kh}{n^2}, \quad (36)$$

where  $h$  is PLANCK'S constant which enters in the fundamental relation (1).

Now according to RUTHERFORD'S theory of atomic structure, a neutral hydrogen atom must be expected to consist of an electron and a positive nucleus of a mass very large compared with that of the electron, which move under the influence of a mutual attraction inversely proportional to the square of the distance apart. Assuming that the motion in the stationary states may be determined by ordinary mechanics, and neglecting for the moment the small modifications claimed by the theory of relativity, we find that each of the particles will describe an elliptical orbit with their common centre of gravity at one of the foci, and from the well known laws for a Keplerian motion we have that the frequency of revolution  $\omega$  and the major axis  $2a$  of the relative orbit of the particles, quite independent of the degree of eccentricity of this orbit, are given by

$$\omega = \sqrt{\frac{2W^3(M+m)}{\pi^2 N^2 e^4 Mm}}, \quad 2a = \frac{Ne^2}{W}, \quad (37)$$

where  $W$  is the work necessary to remove the electron to infinite distance from the nucleus, while  $Ne$  and  $M$  are the charge and the mass of the nucleus, and  $-e$  and  $m$  the charge and the mass of the electron.

As explained in Part I, there will in general be no simple connection between the motion of a system in the stationary states and the spectrum emitted during transitions between these states; such a connection, however, must be expected to exist in the limit where the motions in successive stationary states differ comparatively little from each other. In the present case this connection claims in the first place that the frequency of revolution tends to zero for increasing  $n$ . According to (36) and (37) we may therefore put the value of  $W$  in the  $n^{\text{th}}$  stationary state equal to

$$W_n = \frac{Kh}{n^2}. \quad (38)$$

Moreover, since (35) can be written in the form

$$\nu = (n' - n'') K \frac{n' + n''}{n'^2 n''^2},$$

it is seen to be a necessary condition that the frequency of revolution for large values of  $n$  is asymptotically given by

$$\omega_n \approx \frac{2K}{n^3}, \quad (39)$$

if we wish that the frequency of the radiation emitted during a transition between two stationary states, for which the numbers  $n'$  and  $n''$  are large compared with their difference  $n' - n''$ , shall tend to coincide with one of the frequencies of the spectrum which on ordinary electrodynamics would be emitted from the system in these states. But from (37) and (38) it will be seen that (39) claims the fulfilment of the relation

$$K = \frac{2\pi^2 N^2 e^4 M m}{h^3 (M + m)} = \frac{2\pi^2 N^2 e^4 m}{h^3 (1 + m/M)}. \quad (40)$$

As shown in previous papers, this relation is actually found to be fulfilled within the limit of experimental errors if we put  $N = 1$  and for  $e$ ,  $m$ , and  $h$  introduce the values deduced from measurements on other phenomena; a result which may be considered as affording a strong support for the validity of the general principles discussed in Part I, as well as for the reality of the atomic model under consideration. Further it was found that, if in formula (35) for the hydrogen spectrum the constant  $K$  is replaced by a constant which is four times larger, this formula represents to a high degree of approximation the frequencies of the lines of a spectrum emitted by helium, when this gas is subject to a condensed discharge. This was to be expected on RUTHERFORD'S theory, according to which a neutral helium atom contains two electrons and a nucleus of a charge twice that of the nucleus of the hydrogen atom. A helium atom from which one electron is removed will thus form a dynamical system perfectly similar to a neutral hydrogen atom, and may therefore be expected to emit a spectrum represented by (35) if in (40) we put  $N = 2$ . Moreover a closer comparison of the helium spectrum under consideration

with the hydrogen spectrum has shown that the value of the constant  $K$  in the former spectrum was not exactly four times as large as that in the latter, but that the ratio between these constants within the limit of experimental errors agreed with the value to be expected from (40), when regard is taken to the different masses of the nuclei of the atoms of hydrogen and helium corresponding to the different atomic weights of these elements<sup>1</sup>).

Introducing the expression for  $K$  given by (40) in the formulæ (37) and (38), we find for the values of  $W$ ,  $\omega$  and  $2a$  in the stationary states

$$W_n = \frac{1}{n^2} \frac{2\pi^2 N^2 e^4 Mm}{h^2 (M+m)}, \quad \omega_n = \frac{1}{n^3} \frac{4\pi^2 N^2 e^4 Mm}{h^3 (M+m)}, \quad 2a_n = n^2 \frac{h^2 (M+m)}{2\pi^2 N e^2 Mm}. \quad (41)$$

Now for a mechanical system as that under consideration, for which every motion is periodic independent of the initial conditions, we have that the value of the total energy will be completely determined by the value of the quantity  $I$ , defined by equation (5) in Part I. As mentioned this follows directly from relation (8), which shows at the same time that for a system for which every motion is periodic the frequency will be completely determined by  $I$  or by the energy only. For the value of  $I$  in the stationary states of the hydrogen atom we get by means of (8) from (37) and (41), since in this case  $I$  will obviously become zero when  $W$  becomes infinite,

$$I = \int_{W_n}^{\infty} \frac{dW}{\omega} = \sqrt{\frac{\pi^2 N^2 e^4 Mm}{2(M+m)}} \int_{W_n}^{\infty} W^{-3/2} dW = \sqrt{\frac{2\pi^2 N^2 e^4 Mm}{W_n(M+m)}} = nh.$$

This result will be seen to be consistent with condition (24) which, as mentioned in Part I, presents itself as a direct generalisation to periodic systems of several degrees of freedom of condition (10) which determines the stationary states of a system of one degree of freedom, and which again on EHRENFEST's principle of the mechanical transformability of the stationary states forms a rational generalisation of PLANCK's fundamental formula (9) for the possible values of the energy of a linear harmonic vibrator.

In this connection it will be observed, that the relation discussed above between the hydrogen spectrum and the motion of the atom in the limit of small frequencies is completely analogous to the general relation, discussed in § 2 in Part I, between the spectrum which on the quantum theory would be emitted by a system of one degree of freedom, the stationary states of which are determined by (10), and the motion of the system in these states. It will at the same time be noted that, in case of hydrogen, this relation implies that the motion of the particles in the stationary states of the atom will not in general be simply harmonic, or in other words that the orbit of the electron will not in general be circular. In fact if the motion of the particles were simply harmonic, as the motion of a PLANCK's vibrator,

<sup>1</sup>) For the literature on this subject the reader is referred to the papers cited in the introduction.



we should expect on the considerations in Part I that no transition between two stationary states of the atom would be possible for which  $n'$  and  $n''$  differ by more than one unit; but this would obviously be inconsistent with the observations, since for instance the lines of the ordinary Balmer series, according to the theory, correspond to transitions for which  $n'' = 2$  while  $n'$  takes the values 3, 4, 5, ... In connection with this consideration it may be remarked that, adopting a terminology well known from acoustics, we may from the point of view of the quantum theory regard the higher members of the Balmer series ( $n' = 4, 5, \dots$ ) as the "harmonics" of the first member ( $n' = 3$ ), although of course the frequencies of the former lines are by no means entire multipla of the frequency of the latter line.

While in the above way it was possible to obtain a simple interpretation of certain main features of the hydrogen spectrum, it was not found possible in this way to account in detail for such phenomena in which the deviation of the motion of the particles from a simple Keplerian motion plays an essential part. This is the case in the problem of the fine structure of the hydrogen lines, which is due to the effect of the small variation of the mass of the electron with its velocity, as well as in the problems of the characteristic effects of external electric and magnetic fields on the hydrogen lines. As mentioned in the introduction, a progress of fundamental importance in the treatment of such problems was made by SOMMERFELD, who obtained a convincing explanation of the fine structure of the hydrogen lines by means of his theory of the stationary states of central systems, in which the single condition  $I = nh$  was replaced by the two conditions (16); and the theory was further developed by EPSTEIN and SCHWARZSCHILD, who on this line established the general theory, based on the conditions (22), of the stationary states of a conditionally periodic system for which the equations of motion may be solved by means of separation of variables in the Hamilton-Jacobi partial differential equation. If the hydrogen atom is exposed to a homogeneous electric or to a homogeneous magnetic field, the atom forms a system of this class, and, as shown by EPSTEIN and SCHWARZSCHILD as regards the STARK effect and by SOMMERFELD and DEBYE as regards the ZEEMAN effect, the theory under consideration leads to values for the total energy of the atom in the stationary states, which together with relation (1) lead again to values for the frequencies of the radiations emitted during the transitions between these states, which are in agreement with the measured frequencies of the components into which the hydrogen lines are split up in the presence of the fields. As pointed out in Part I, it is possible moreover to throw light on the question of the intensities and polarisations of these components on the basis of the necessary formal relation between the quantum theory of line spectra and the ordinary theory of radiation in the limit where the motions in successive stationary states differ very little from each other. In the following sections the mentioned problems will be discussed in detail. As regards the fixation of the stationary states we shall not, however, follow the same procedure as used by the authors just mentioned, which rests upon the immediate application of the conditions

(22), but it will be shown how the conditions which fix the stationary states of the perturbed atom may be obtained by a direct examination of the small deviations of the motion of the electron from a simple Keplerian motion. In this way it seems possible to obtain a more direct illustration of the principles discussed in Part I; and we shall see moreover that the treatment in question may be used also in cases where the method of separation of variables cannot be applied.

In Part III the problem of the series spectra of other elements will be treated from a similar point of view. As pointed out by the writer in an earlier paper, a simple explanation of the pronounced analogy between these spectra and the hydrogen spectrum is offered by the fact, that the atomic systems, involved in the emission of the spectra under consideration, in a certain sense may be regarded as a perturbed hydrogen atom. On the other hand, a clue to the interpretation of the characteristic difference between the hydrogen spectrum and the spectra of other elements was first obtained by SOMMERFELD's theory of the stationary states of central systems referred to above. As shown by SOMMERFELD, it is possible on this theory to account in general outlines for the well known laws governing the frequencies of the series spectra of the elements; and, as it will be shown in Part III, it is also possible, on the basis of the formal relation between the quantum theory and the ordinary theory of radiation, in this way to obtain a simple interpretation of the laws governing the remarkable differences in the intensities with which the various series of lines appear, which on the combination principle would constitute the complete spectra under consideration. As regards the detailed discussion of these spectra, however, it is necessary to bear in mind that the part played by the inner electrons in the atoms of the elements in question forms a far more intricate problem than the perturbing effect of a fixed external field on the hydrogen atom. For the treatment of this problem the theory of conditionally periodic systems based on the conditions (22) does not seem to suffice, while, as it will be shown in Part III, it appears that the method of perturbations exposed in the following lends itself naturally also to this case.

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## § 2. The stationary states of a perturbed periodic system.

In Part I it was shown that the problem of the fixation of the stationary states of a periodic system of several degrees of freedom, which is subject to the perturbing influence of a small external field, cannot be treated directly on the basis of the general principle of the mechanical transformability of the stationary states by considering the influence, which on ordinary mechanics a slow establishment of the external field would exert on the motion of some arbitrarily chosen stationary state of the undisturbed system (see Part I, p. 23). This is an immediate consequence of the fact, mentioned in the former section, that the stationary states

of the perturbed system are characterised by a greater number of extra-mechanical conditions than the stationary states of the undisturbed system. On the other hand, we were led to assume from the general formal relation between the quantum theory of line spectra and the ordinary theory of radiation, that it is possible to obtain information about the stationary states of the perturbed system from a direct consideration of the slow variations which the periodic orbit undergoes as a consequence of the mechanical effect of the external field on the motion. Thus, if these variations are of periodic or conditionally periodic type, we may expect that, in the presence of the external field, the values for the additional energy of the system in the stationary states are related to the small frequency or frequencies of the perturbations, in a manner analogous to the relation between energy and frequency in the stationary states of an ordinary periodic or conditionally periodic system.

If the equations of motion for the perturbed system can be solved by means of separation of variables, it is easily seen that the relation in question is fulfilled if the stationary states are determined by the conditions (22). Consider thus a system for which every orbit is periodic, and let us assume that in the presence of a given small external field a separation of variables is possible in a certain set of coordinates  $q_1, \dots, q_s$ . For the undisturbed system we have then, according to equation (23), that the quantity  $I$ , defined by (5), is equal to  $z_1 I_1 + \dots + z_s I_s$ , where  $I_1, \dots, I_s$  are defined by (21) and calculated with respect to the set of coordinates just mentioned, and where the  $z$ 's are a set of entire positive numbers without a common divisor. For simplicity let us assume that at least one of the  $z$ 's, say  $z_s$ , is equal to one, and that consequently, as mentioned on page 22, the number  $n$  in (24), which characterises the stationary states of the undisturbed system, may take all positive values. This condition will be fulfilled in case of all the applications to spectral problems discussed below; it will be seen, however, that the extension to problems where this condition is not fulfilled will only necessitate small modifications in the following considerations. By use of (29) we get now for the difference in the total energy of two slightly different states of the perturbed system

$$\partial E = \sum_1^s \omega_k \partial I_k = \omega_s \sum_1^s z_k \partial I_k + \sum_1^{s-1} (\omega_k - z_k \omega_s) \partial I_k. \quad (42)$$

Since for the undisturbed system  $\omega_k = z_k \omega_s$ , the differences  $\omega_k - z_k \omega_s$  appearing in the last term will, for the perturbed system, be small quantities which will just represent the frequencies of the slow variations which the orbit undergoes in the presence of the external field. These quantities will in the following be denoted by  $\nu_k$ . Consider now the multitude of states of the perturbed system for which  $\sum_1^s z_k I_k$  is equal to  $nh$ , where  $n$  is a given entire positive number. This multitude will be seen to include all possible stationary states of the perturbed system, which satisfy (22), and the motion of which differs at any moment only slightly from some stationary motion of the undisturbed system, satisfying (24) for the given value of



$n$ . Denoting the value of the energy of the undisturbed system in such a state by  $E_n$ , and the value of the energy of the perturbed system in a state belonging to the multitude under consideration by  $E_n + \mathfrak{E}$ , we get from (42)

$$\delta \mathfrak{E} = \sum_{k=1}^{s-1} \nu_k \delta I_k \quad (43)$$

for the energy difference between two neighbouring states of this multitude. Since this relation has the same form as (29), we see consequently that by putting  $I_1, \dots, I_{s-1}$  equal to entire multipla of  $h$ , as claimed by the conditions (22), we obtain exactly the same relation between the additional energy  $\mathfrak{E}$  and the small frequencies  $\nu_k$ , impressed on the system by the external field, as that which holds between the total energy and the fundamental frequencies in the stationary states of a conditionally periodic system of  $s-1$  degrees of freedom.

As a simple illustration of these calculations let us consider the system consisting of a particle moving in a plane and subject to an attraction from a fixed point, which varies proportional to the distance apart. If undisturbed, the motion of this system will be periodic independent of the initial conditions, and the particle will describe an elliptical orbit with its centre at the fixed point. Moreover the equations of motion of the undisturbed system may be solved by means of separation of variables in polar coordinates, as well as in any set of rectangular coordinates. In the first case we have, taking for  $q_1$  the length of the radius vector from the fixed point to the particle and for  $q_2$  the angular distance of this radius vector from a fixed direction,  $\alpha_1 = 2$  and  $\alpha_2 = 1$ , while in the second case we have  $\alpha_1 = \alpha_2 = 1$ . In the presence of an external field the orbit will in general not remain periodic, but will in the course of time cover a continuous extension of the plane. If the external field is sufficiently small, however, the orbit will at any moment only differ little from a closed elliptical orbit, but in the course of time the lengths and directions of the principal axes of this ellipse will undergo slow variations. In general the perturbed system will not allow of separation of variables, but two cases obviously present themselves in which such a separation is still possible; in the first case the external field is central with the fixed point as centre, and a separation is possible in polar coordinates; in the second case the external field of force is perpendicular to a given line and varies as some function of the distance from this line, and separation is possible in a set of rectangular coordinates with the axes parallel and perpendicular to the given line. In the first case the perturbations will not affect the lengths of the principal axes of the elliptical orbit and will only produce a slow uniform rotation of the directions of these axes, while in the second case the lengths of the principal axes as well as their directions will perform slow oscillations. It will consequently be seen that, by fixing the stationary states of the perturbed system by means of the conditions (22), the cycles of shapes and positions which the orbit of the particle will pass through in the stationary states will be entirely different in the two cases. In both cases, however, it will be seen that the frequency  $\nu = \omega_1 - \alpha_1 \omega_2$  will be equal to the frequency with which the orbit at regular intervals re-assumes its shape and position. By fixing the stationary states by (22) we obtain therefore, as seen from (43), in both cases that the relation between this frequency and the additional energy of the system due to the presence of the field will be the same as the relation between energy and frequency in the stationary states of a system of one degree of freedom; and it will be seen that the above considerations offer a dynamical interpretation of the characteristic discontinuity involved in the application of the method of separation of variables to the fixation of the stationary states of perturbed periodic systems<sup>1)</sup>.

<sup>1)</sup> In this connection it may be of interest to note that the possibility of a rational interpretation of

In general it will not be possible to solve the equations of motion of the perturbed system by means of separation of variables in a fixed set of positional coordinates, but we shall see that the problem of the fixation of the stationary states of the perturbed system may be attacked by a direct examination of the additional energy of the system and its relation to the slow variations of the orbit, on the basis of the usual theory of perturbations well known from celestial mechanics. Consider a system for which every orbit, if undisturbed, is periodic independent of the initial conditions, and let us assume that the equations of motion for some set of coordinates  $q_1, q_2, \dots, q_s$  are solved by means of the Hamilton-Jacobi partial differential equation, given by formula (17) in Part I. The motion of the system is then determined by the equations (18), and the orbit is characterised by means of the constants  $a_1, \dots, a_s, \beta_1, \dots, \beta_s$ . If now the system is subject to some small external field of force, the motion will no more be periodic, but, defining in the usual way the osculating orbit at a given moment as the periodic orbit which would result if the external forces vanished suddenly at this moment, we find that the constants  $a_1, \dots, a_s, \beta_1, \dots, \beta_s$ , characterising the osculating orbit, will vary slowly with the time. Assuming for the present that the external forces possess a constant potential  $\mathcal{Q}$  given as a function of the  $q$ 's, we have according to the theory of perturbations that the rates of variation of the orbital constants of the osculating orbit will be given by<sup>1)</sup>

$$\frac{da_k}{dt} = -\frac{\partial \mathcal{Q}}{\partial \beta_k}, \quad \frac{d\beta_k}{dt} = \frac{\partial \mathcal{Q}}{\partial a_k}, \quad (k = 1, \dots, s) \quad (44)$$

where  $\mathcal{Q}$  is considered as a function of  $a_1, \dots, a_s, \beta_1, \dots, \beta_s$  and  $t$ , obtained by introducing for the  $q$ 's their expressions as functions of these quantities obtained by solving (18). The equations (44) allow to follow completely the perturbing effect of the external field on the motion of the system. For the problem under consideration, however, a detailed examination of the perturbations is not necessary. In fact, we shall not be concerned with the small deformation of the orbit characterised by the small oscillations of the orbital constants within a time interval of the same order of magnitude as the period of the osculating orbit, but only

the discontinuity in question would seem to be essentially connected with the form of the principles of the quantum theory adopted in this paper. If for instance the quantum theory is taken in the form proposed by PLANCK in his second theory of temperature radiation, the consequent development to periodic systems of several degrees of freedom would seem to involve a serious difficulty as regards the question of the necessary stability of the temperature equilibrium among a great number of systems for small variations of the external conditions. In fact, in connection with the development of his theory of the "physical structure of the phase space", mentioned in Part I on page 18, in which conditions of the same type as (22) are established, PLANCK has deduced expressions for the total energy of a great number of systems in temperature equilibrium, which, if applied to systems of the same kind as those considered in the above example, show a dependency of this energy on the temperature which is different, according to whether polar coordinates or rectangular coordinates are used as basis for the structure of the phase space.

<sup>1)</sup> See f. inst. C. V. L. CHARLIER, *Die Mechanik des Himmels*, Bd. I, Abt. 1, § 10.

with the so-called "secular perturbations" of the orbit, characterised by the total variation of these constants taken over a time interval long compared with the period of the osculating orbit. As we shall see below, these variations may, with an approximation sufficient for our purpose, be obtained directly by taking mean values on both sides of the equations (44). Before entering on these calculations, however, it may be observed that the part played by the constants  $a_1$  and  $\beta_1$  differs essentially from that played by the other orbital constants  $a_2, \dots, a_s, \beta_2, \dots, \beta_s$ . Thus from the formulæ (17) and (18) on page 19, it follows that  $a_1$  is the total energy corresponding to the osculating orbit, while  $\beta_1$  will represent the moment in which the system would pass some distinguished point in this orbit. If for instance we consider the perturbations of a Keplerian motion, we may for  $\beta_1$  take the so called time of perihelium passage. When discussing the secular perturbations of the shape and position of the orbit, we see therefore in the first place that the variations of  $\beta_1$  may be left out of consideration. Further, it follows from the principle of conservation of energy, that  $a_1 + Q$  will remain constant during the motion, and that consequently during the perturbations  $a_1$  will change only by small quantities of the same order as  $\lambda a_1$ , where  $\lambda$  denotes a small constant of the same order of magnitude as the ratio between the external forces and the internal forces of the system. Moreover, since the period  $\sigma$  of the undisturbed motion depends on  $a_1$  only, it follows that the period of the osculating orbit will remain constant during the perturbations, with neglect of small quantities of the same order as  $\lambda\sigma$ . On the other hand it follows from (44) that, in a time interval of the same order as  $\sigma/\lambda$ , the constants  $a_2, \dots, a_s, \beta_2, \dots, \beta_s$  will in general undergo variations of the same order of magnitude as the values of these constants themselves.

As mentioned above, the total variations of the constants  $a_2, \dots, a_s, \beta_2, \dots, \beta_s$ , which characterise the secular perturbations of the shape and position of the orbit, may be obtained by taking mean values on both sides of the equations (44). Introducing a function  $\Psi$  of the  $a$ 's and  $\beta$ 's, equal to the mean value of the potential  $Q$  taken over a period  $\sigma$  of the motion of the undisturbed system and defined by the formula

$$\Psi = \frac{1}{\sigma} \int_t^{t+\sigma} Q dt, \quad (45)$$

it is easily seen, since  $\sigma$  depends only on  $a_1$ , that the mean values of the partial differential coefficients of  $Q$  with respect to  $a_2, \dots, a_s, \beta_2, \dots, \beta_s$ , taken over an approximate period of the perturbed motion, may, if we look apart from small quantities proportional to  $\lambda^2$ , be replaced by the values of the corresponding partial differential coefficients of  $\Psi$  at some moment within this period. With the approximation mentioned we get therefore

$$\frac{D a_k}{D t} = - \frac{\partial \Psi}{\partial \beta_k}, \quad \frac{D \beta_k}{D t} = \frac{\partial \Psi}{\partial a_k}, \quad (k = 2, \dots, s) \quad (46)$$



where the differential symbols on the left sides are written to indicate mean values of the rates of variation of the orbital constants during an approximate period of the perturbed motion. From the definition of  $\Psi$  it follows that this quantity in general will depend on  $a_1$  as well as on  $a_2, \dots, a_s, \beta_2, \dots, \beta_s$ , but that it will not depend upon  $\beta_1$ . From the above considerations it follows further that, with the approximation in question,  $a_1$  may be considered as a constant in the expressions on the right sides of (46), while for  $a_2, \dots, a_s, \beta_2, \dots, \beta_s$  we may take a set of values corresponding to some moment within the period to which the mean values on the left sides refer.

It will be seen that the equations (46) allow to follow the secular perturbations during a time interval sufficiently long for the external forces to produce a considerable change in the shape and position of the original orbit, if in the total variations of the orbital constants  $a_2, \dots, a_s, \beta_2, \dots, \beta_s$  we look apart from small quantities of the same order as the small oscillations of these constants within a single period. As a consequence of the secular variations, the orbit will pass through a cycle of shapes and positions, which will depend on its original shape and position and on the character of the perturbing field, but not on the intensity of this field. In fact, as seen from (46), the variations in the shape and position of the orbit will remain the same if  $\Psi$  is multiplied by a constant factor, which will only influence the rate at which these variations are performed. It will further be observed that the problem of determining the secular perturbations by means of (46) consists in solving a set of equations of the same type as the Hamiltonian equations of motion for a system of  $s-1$  degrees of freedom. In these equations the quantity  $\Psi$  plays formally the same part as the total energy in the usual mechanical problem, and in analogy with the principle of conservation of energy it follows directly from (46) that, with neglect of small quantities proportional to  $\lambda^2$ , the value of  $\Psi$  will remain constant during the perturbations, even if the external forces act through a time interval of the same order as  $\sigma/\lambda$ . In fact, with neglect of small quantities proportional to  $\lambda^3$ , we have

$$\frac{D\Psi}{Dt} = \sum_2^s \left( \frac{\partial \Psi}{\partial a_k} \frac{Da_k}{Dt} - \frac{\partial \Psi}{\partial \beta_k} \frac{D\beta_k}{Dt} \right) = \sum_2^s \left( -\frac{\partial \Psi}{\partial a_k} \frac{\partial \Psi}{\partial \beta_k} + \frac{\partial \Psi}{\partial \beta_k} \frac{\partial \Psi}{\partial a_k} \right) = 0.$$

Since at any moment  $\Psi$  will differ only by small quantities proportional to  $\lambda^2$  from the mean value of the potential of the external forces taken over an approximate period of the perturbed motion, it follows from the above that, with neglect of small quantities of this order, also the mean value of the inner energy  $a_1$  of the perturbed system, taken over an approximate period, will remain constant during the perturbations, even if the perturbing forces act through a time interval long enough to produce a considerable change in the shape and position of the orbit. In the special case, where the perturbed system allows of separation of variables, this last result may be shown to follow directly from formula (28) in Part I. Taking for the time interval  $\vartheta$  in this formula the period  $\sigma$  of the undisturbed

motion, we get  $N_k = z_k$ , where  $z_1, \dots, z_s$  are the numbers entering in formula (23). Comparing a given perturbed motion of the system with some undisturbed motion of which it may be regarded as a small variation, we get therefore from (28), with neglect of small quantities proportional to the square of the intensity of the external forces,

$$\int_0^\sigma \partial E dt = \sum_1^s z_k \partial I_k, \quad (47)$$

where the  $I$ 's are calculated with respect to a set of coordinates in which a separation can be obtained for the perturbed motion, and where  $\partial E$  is the difference between the total energy of the undisturbed motion and the energy which the system would possess in its perturbed state, if the external forces vanished suddenly at the moment under consideration, and which in the above calculations was denoted by  $a_1$ . Now the energy  $E$  of the undisturbed motion is determined completely by the value of  $I = \sum z_k I_k$ . If therefore the perturbed motion is all the time compared with a neighbouring undisturbed motion of given constant energy, it follows directly from (47), that, with neglect of small quantities of the same order as the square of the external forces, the integral on the left side, taken over an approximate period of the perturbed motion, will remain unaltered during the perturbations through any time interval, however long.

Before proceeding with the applications of the equations (46) which apply to the case of a constant perturbing field, it will be necessary to consider the effect of a slow and uniform establishment of the external field. Let us assume that, within the interval  $0 < t < \vartheta$  where  $\vartheta$  denotes a quantity of the same order as  $\sigma/\lambda$ , the intensity of the external field increases uniformly from zero to the value corresponding to the potential  $\mathcal{Q}$ . Since the variation in the perturbing field during a single period will only be a small quantity of the same order as  $\lambda^2$ , we see in the first place that the secular variations of the constants  $\alpha_2, \dots, \alpha_s, \beta_2, \dots, \beta_s$ , with the same approximation as for a constant field, will be given by a set of equations of the same form as (46), with the only difference that  $\mathcal{V}$  is replaced by  $\frac{t}{\vartheta} \mathcal{V}$ . Moreover it may be shown that in these equations the quantity  $a_1$  may be considered as constant, just as in the equations which hold for a constant perturbing field. In fact the total variation in  $a_1$  at any moment  $t$  will be equal to the total work performed by the external forces since the beginning of the establishment of the perturbing field, and will therefore be given by

$$\Delta_t a_1 = - \int_0^t \frac{t}{\vartheta} \sum_1^s \frac{\partial \mathcal{Q}}{\partial q_k} \dot{q}_k dt = \frac{1}{\vartheta} \int_0^t \mathcal{Q} dt - \frac{t}{\vartheta} \mathcal{Q}_t, \quad (48)$$

where the expression on the right side is obtained by partial integration; but, since both terms in this expression are of the same order of magnitude as  $\lambda a_1$ , we see that the

total variation in  $\alpha_1$  within the interval in question will, just as in case of a constant perturbing field, be only a small quantity of this order. We get therefore the result, that, for the same shape and position of the original orbit, the cycle of shapes and positions passed through by the orbit during the increase of the external field will be the same as that which would appear for a constant perturbing field, and that, with neglect of small quantities proportional to  $\lambda^2$ , the value of the function  $\mathcal{V}$  will consequently remain constant during the establishment of the field. With this approximation we get therefore from (48), putting  $t = \vartheta$ ,

$$\Delta_{\vartheta} \alpha_1 + \mathcal{Q}_{\vartheta} = \frac{1}{\vartheta} \int_0^{\vartheta} \mathcal{Q} dt = \mathcal{V},$$

which shows that the change in the total energy of the system, due to the slow and uniform establishment of the external field, is just equal to the value of the function  $\mathcal{V}$ ; and consequently equal to the mean value of the potential of the external forces taken over an approximate period of the perturbed motion. This result may also be expressed by stating, that, with neglect of small quantities proportional to the square of the external forces, the mean value of the inner energy taken over an approximate period of the perturbed motion will be equal to the energy possessed by the system before the establishment of the perturbing field.

Returning now to the problem of the fixation of the stationary states of a periodic system subject to the influence of a small external field of constant potential, we shall base our considerations on the fundamental assumption that these states are distinguished between the continuous multitude of mechanically possible states by a relation between the additional energy of the system due to the presence of the external field and the frequencies of the slow variations of the orbit produced by this field, which is analogous to the relation discussed on page 42 in the special case in which the perturbed system allows of separation of variables in a fixed set of coordinates. On this assumption we shall expect in the first place that, apart from small quantities proportional to  $\lambda$ , the cycles of shapes and positions of the orbit belonging to the stationary states of the perturbed system will depend only on the character of the external field, but not on its intensity. Since now, as shown above, such a cycle will remain unaltered during a slow and uniform increase of the intensity of the external field if the effect of the external forces is calculated by means of ordinary mechanics, we are therefore, with reference to the principle of the mechanical transformability of the stationary states, led to the conclusion that it is possible by direct application of ordinary mechanics, not only to follow the secular perturbations of the orbit in the stationary states corresponding to a constant external field, but also to calculate the variation in the energy of the system in the stationary states which results from a slow and uniform change in the intensity of this field. If we denote the energy in the stationary states of the perturbed system by  $E_n + \mathcal{E}$ , where  $E_n$  is the value of the energy in the stationary state of the un-



disturbed system characterised by a given entire value of  $n$  in the condition  $I = nh$ , we may therefore conclude from the above that the additional energy  $\mathfrak{E}$  in the stationary states of the perturbed system will be equal to the value in these states of the function  $\mathcal{V}$  defined by (45), if we look apart from small quantities proportional to the square of the intensity of the external forces. It will be seen that this result is equivalent to the statement, that the mean value of the inner energy taken over an approximate period of the perturbed motion will be equal to the value  $E_n$  of the energy in the corresponding stationary state of the undisturbed system. In case of the perturbed system allowing of separation of variables in a fixed set of coordinates, this result may be simply shown to be a direct consequence of the fixation of the stationary states by means of the conditions (22). In fact, if we assume that the undisturbed motion, considered in (47), corresponds to some stationary state, satisfying (24) for a given value of  $n$ , and that the perturbed motion is also stationary and satisfies (22), we see that the right side of (47) will be zero, and we get the result that the mean value of the inner energy in the stationary states of the system, with the approximation mentioned, will not be altered in the presence of the external field.

Due to the above result that the additional energy  $\mathfrak{E}$  in the stationary states of the perturbed system, with neglect of small quantities proportional to  $\lambda^2$ , may be taken equal to the value in these states of the function  $\mathcal{V}$  entering in the equations (46) which determine the secular perturbations of the orbits, we are now able to draw further conclusions from the fact, mentioned above, that these equations are of the same type as the Hamiltonian equations of motion for a mechanical system of  $s-1$  degrees of freedom. In fact, we see that the fixation of the stationary states of the perturbed system is reduced to a problem which is formally analogous to the fixation of these states for a mechanical system of less degrees of freedom. As it will appear from the following applications this problem may, quite independent of the possibility of separation of variables for the perturbed system, be treated directly on the basis of the fundamental relation between energy and frequency in the stationary states of periodic or conditionally periodic systems, discussed in Part I, if only the solution of the equations (46) is of a periodic or conditionally periodic character. In this connection it may once more be emphasised that these equations, according to the manner in which they were deduced, allow to follow the secular perturbations only through a time interval of the same order of magnitude as that sufficient for the external forces to produce a finite alteration in the shape and position of the orbit. With reference to the necessary stability of the stationary states of an atomic system, it seems justified, however, to conclude that any possible small discrepancy between the motion to be expected from a rigorous application of ordinary mechanics and that determined by a calculation of the secular perturbations, based on the equations (46), cannot cause a material change in the character of the stationary states as fixed by a consideration of the periodicity properties of these perturbations. On the

other hand, from the point of view of the general formal relation between the quantum theory and the ordinary theory of radiation, we must be prepared to find that the motion and the energy in the stationary states of a perturbed periodic system, for which we only know that the secular perturbations as determined by (46) are of conditionally periodic type, will not be as sharply defined as the motion and the energy in the stationary states of a conditionally periodic system for which the equations of motion allow of a rigorous solution by means of the method of separation of variables. Thus, if we consider a large number of similar atomic systems of the type in question, we may be prepared to find that the values of the additional energy in a given stationary state will for the different systems deviate from each other by small quantities; but it must be expected that the values of the additional energy for the large majority of systems will differ from the value of  $\Psi$ , as determined by the method indicated above, only by small quantities proportional to  $\lambda^2$ , and that only for a small fraction (at most of the same order as  $\lambda^2$ ) of the systems the values of the additional energy will show deviations from this value of  $\Psi$ , which are of the same order as  $\lambda$ .

As to the application of the preceding considerations to special problems, it will be seen in the first place that in case of a perturbed periodic system possessing two degrees of freedom, as for instance that considered in the example on page 43, the problem of the fixation of the stationary states of the perturbed system in the presence of a small external field allows of a general solution on the basis of the method developed above, because in this case the secular perturbations will in general be simply periodic. In fact, in this case the shape and position of the orbit are characterised by two constants  $a_2$  and  $\beta_2$ , and from the equations (46), which will be analogous to the equations of motion of a system of one degree of freedom, it follows directly that during the perturbations  $a_2$  will be a function of  $\beta_2$  and that in general these quantities will be periodic functions of the time with a period  $\mathfrak{s}$  which, besides on  $a_1$ , will depend on the value of  $\Psi$  only. Considering two slightly different states of the perturbed system for which the corresponding states of the undisturbed system (i. e. the states which would appear if the external forces vanished at a slow and uniform rate) possess the same energy and consequently the same value for the quantity  $I$  defined by (5), we get therefore by a calculation completely analogous to that leading to relation (8) in Part I, which was deduced directly from the Hamiltonian equations, for the difference in the values of the function  $\Psi$  for these two states

$$\delta\Psi = \nu\delta\mathfrak{S}, \quad (49)$$

where  $\nu = \frac{1}{\mathfrak{s}}$  is the frequency of the secular perturbations, and where the quantity  $\mathfrak{S}$  is defined by

$$\mathfrak{S} = \int_0^{\mathfrak{s}} a_2 \frac{D\beta_2}{Dt} dt = \int a_2 D\beta_2, \quad (50)$$

where the latter integral is taken over a complete oscillation of  $\beta_2$ . In order to fix the stationary states, it will now be seen in the first place that, among the multitude of states of the perturbed system for which the value of  $I$  in the corresponding states of the undisturbed system is equal to  $nh$  where  $n$  is a given positive integer, the state for which  $\mathfrak{F} = 0$  must beforehand be expected to be a stationary state. In fact, for this value of  $\mathfrak{F}$ , the shape and position of the orbit will not undergo secular perturbations but will remain unaltered for a constant external field as well as during a slow and uniform establishment of this field. In contrast to what in general will take place during a slow establishment of the external field, we may therefore expect that, for this special shape and position of the orbit, a direct application of ordinary mechanics will be legitimate in calculating the effect of the establishment of the field, since there will in this case obviously be nothing to cause the coming into play of some non-mechanical process, connected with the mechanism of a transition between two stationary states accompanied by the emission or absorption of a radiation of small frequency. With reference to relation (49) we see therefore that, by fixing the stationary states of the perturbed system by means of the condition

$$\mathfrak{F} = nh, \quad (51)$$

where  $n$  is an entire number, we obtain a relation between the additional energy  $\mathfrak{E} = \mathcal{V}'$  of the system in the presence of the field and the frequency  $\nu$  of the secular perturbations, which is exactly of the same type as that which holds between the energy and frequency in the stationary states of a system of one degree of freedom, and which is expressed by (8) and (10). By means of (51) it is possible, with neglect of small quantities proportional to the square of the perturbing forces, directly to determine the value of the additional energy in the stationary states of a periodic system of two degrees of freedom subject to an arbitrarily given small external field of force, and consequently with this approximation, by use of the fundamental relation (1), to determine the effect of this field on the frequencies of the spectrum of the undisturbed periodic system. In general this effect will consist in a splitting up of each of the spectral lines into a number of components which are displaced from the original position of the line by small quantities proportional to the intensity of the external forces.

When we pass to perturbed periodic systems of more than two degrees of freedom, the general problem is more complex. For a given external field, however, it may be possible to choose a set of orbital constants  $\alpha_2, \dots, \alpha_s, \beta_2, \dots, \beta_s$  in such a way, that during the motion every of the  $\alpha$ 's will depend on the corresponding  $\beta$  only, while every of the  $\beta$ 's will oscillate between two fixed limits. From analogy with the theory of ordinary conditionally periodic systems which allow of separation of variables, the perturbations may in such a case be said to be conditionally periodic, and, from a calculation quite analogous to that leading to equation (29) in Part I which is based entirely on the use of the Hamiltonian equations, we get for the difference in  $\mathcal{V}'$  for two slightly different states



of the perturbed system, for which the value of  $I$  in the corresponding states of the undisturbed system is the same,

$$\partial \psi = \sum_1^{s-1} \nu_k \partial \mathfrak{F}_k, \quad (52)$$

where  $\nu_k$  is the mean frequency of oscillation of  $\beta_{k+1}$  between its limits, and where the quantities  $\mathfrak{F}_k$  are defined by

$$\mathfrak{F}_k = \int \alpha_{k+1} D\beta_{k+1}, \quad (k = 1, \dots, s-1) \quad (53)$$

where the integral is taken over a complete oscillation of  $\beta_{k+1}$ . In analogy with the expression (31) for the displacements of the particles of an ordinary conditionally periodic system which allows of separation of variables, we get further in the present case that every of the  $\alpha$ 's and  $\beta$ 's may be expressed as a function of the time by a sum of harmonic vibrations of small frequencies

$$\left. \begin{matrix} \alpha \\ \beta \end{matrix} \right\} = \sum \mathfrak{C}_{t_1, \dots, t_{s-1}} \cos 2\pi \{ (t_1 \nu_1 + \dots + t_{s-1} \nu_{s-1}) t + c_{t_1, \dots, t_{s-1}} \}, \quad (54)$$

where the  $\mathfrak{C}$ 's and  $c$ 's are constants, the former of which, besides on  $I$ , depend on the  $\mathfrak{F}$ 's only, and where the summation is to be extended over all positive and negative entire values of the  $t$ 's. If therefore the secular perturbations are conditionally periodic, we may conclude that the stationary states of the perturbed system, corresponding to a given stationary state of the undisturbed system, will be characterised by the  $s-1$  conditions

$$\mathfrak{F}_k = n_k h, \quad (k = 1, \dots, s-1) \quad (55)$$

where  $n_1, \dots, n_{s-1}$  form a set of entire numbers. In fact, as seen from (52), we obtain in this way a relation between the additional energy and the frequencies of the secular perturbations of exactly the same type as that holding for the energy and frequencies of ordinary conditionally periodic systems and expressed by (22) and (29); moreover we may conclude beforehand that the state in which every of the quantities  $\mathfrak{F}_k$ , defined by (53), is equal to zero must belong to the stationary states of the perturbed system, because in this case the orbit will not undergo secular perturbations for a constant external field, nor during a slow and uniform establishment of this field. Since the conditions (55), with neglect of small quantities proportional to the square of the intensities of the external forces, allow to determine the additional energy of the system due to the presence of the external field, we see therefore that the effect of this field on the spectrum of the undisturbed system, if the secular perturbations are conditionally periodic, will consist in a splitting up of each spectral line in a number of components, in analogy with the effect of a perturbing field on the spectrum of a periodic system of two degrees of freedom. In general, however, the perturbations, which a periodic system of more than two degrees of

freedom undergoes in the presence of a given external field, cannot be expected to be conditionally periodic and to exhibit periodicity properties of the type expressed by formula (54). In such cases it seems impossible to define stationary states in a way which leads to a complete fixation of the total energy in these states, and we are therefore led to the conclusion, that the effect of the external field on the spectrum will not consist in the splitting up of the spectral lines of the original system into a number of sharp components, but in a diffusion of these lines over spectral intervals of a width proportional to the intensity of the external forces.

In special cases in which the secular perturbations of a perturbed periodic system of more than two degrees of freedom are of conditionally periodic type, it may occur that these perturbations are characterised by a number of fundamental frequencies, which is less than  $s - 1$ . In such cases, in which the perturbed periodic system from analogy with the terminology used in Part I may be said to be degenerate, the necessary relation between the additional energy and the frequencies of the secular perturbations is secured by a number of conditions less than that given by (55), and the stationary states are consequently characterised by a number of conditions less than  $s$ . With a typical example of such systems we meet if, for a perturbed periodic system of more than two degrees of freedom, the secular perturbations are simply periodic independent of the initial shape and position of the orbit. In direct analogy to what holds for perturbed periodic systems of two degrees of freedom, the difference between the values of  $\Psi$  in two slightly different states of the perturbed system, corresponding to the same value of  $I$ , will in the present case be given by

$$\delta \Psi = \nu \delta \mathfrak{J}, \quad (56)$$

where  $\nu$  is the frequency of the secular perturbations, and where  $\mathfrak{J}$  is defined by

$$\mathfrak{J} = \int_0^{\mathfrak{s}} \sum_2^s a_k \frac{D\beta_k}{Dt} dt, \quad (57)$$

where  $\mathfrak{s} = 1/\nu$  is the period of the perturbations. We may therefore conclude that the stationary states of the perturbed system, corresponding to a given stationary state of the undisturbed system, will be characterised by the single condition

$$\mathfrak{J} = \pi h, \quad (58)$$

in which  $\pi$  is an entire number, and which will be seen to be completely analogous to the condition which fixes the stationary states of ordinary periodic systems of several degrees of freedom.

In the following sections we shall apply the preceding considerations to the problem of the fixation of the stationary states of the hydrogen atom, when the relativity modifications are taken into account, and when the atom is exposed to small external fields. In this discussion we shall for the sake of simpli-

city consider the mass of the nucleus as infinite in the calculations of the perturbations of the orbit of the electron. This involves, in the expression for the additional energy of the system, the neglect of small terms of the same order as the product of the intensity of the external forces with the ratio between the mass of the electron and the mass of the nucleus, but due to the smallness of the latter ratio the error introduced by this simplification will be of no importance in the comparison of the results with the measurements. Since in the case under consideration the system possesses three degrees of freedom, the equations which determine the secular perturbations of the orbit of the electron will correspond to the equations of motion of a system of two degrees of freedom, and it will therefore not be possible to give a general treatment of the problem of the stationary states. Thus, for any given external field, we meet with the question whether the perturbations are conditionally periodic and, if so, in what set of orbital constants this periodicity may be conveniently expressed. Now, in many spectral problems, the external field possesses axial symmetry round an axis through the nucleus, and in this case it is easily shown that the problem of the fixation of the stationary states allows of a general solution. A choice of orbital constants which is suitable for the discussion of this problem, and which is well known from the astronomical theory of planetary perturbations, is obtained by choosing for  $\alpha_2$  the total angular momentum of the electron round the nucleus and for  $\alpha_3$  the component of this angular momentum round the axis of the field. For the set of  $\beta$ 's, corresponding to this set of  $\alpha$ 's, we may take  $\beta_2$  equal to the angle, which the major axis makes with the line in which the plane of the orbit cuts the plane through the nucleus perpendicular to the axis of the field, and  $\beta_3$  equal to the angle between this line and a fixed direction in the latter plane. For the problem under consideration it will be seen that, with this choice of constants, the mean value  $\Psi$  of the potential of the perturbing field will, besides on  $\alpha_1$ , generally depend on  $\alpha_2$  and  $\beta_2$  as well as on  $\alpha_3$ , but due to the symmetry round the axis it will obviously not depend on  $\beta_3$ . In consequence of this, the equations (46), which determine the secular perturbations, will possess the same form as the Hamiltonian equations of motion for a particle moving in a plane and subject to a central field of force. Thus corresponding to the conservation of angular momentum for central systems, we get in the first place from (46) that  $\alpha_3$  will remain unaltered during the perturbations. Next corresponding to the simple periodicity of the radial motion in central systems, we see from (46), if  $\alpha_3$  as well as  $\alpha_1$  is considered as a constant, that during the perturbations  $\alpha_2$  will be a function of  $\beta_2$  and vary in a simple periodic way with the time. The perturbations of the orbit of the electron produced by an external field which possesses axial symmetry will therefore always be of conditionally periodic type, quite independent of the possibility of separation of variables for the perturbed system. As regards the form of the conditions which fix the stationary states, it may be noted, however, that with the choice of orbital constants under consideration the  $\beta$ 's will not, as it was assumed for the sake of simplicity in the general dis-



cussion on page 52, oscillate between fixed limits, but it will be seen that  $\beta_2$  during the perturbations may either oscillate between two such limits or increase (or decrease) continuously, while  $\beta_3$  will always vary in the latter manner. This constitutes, however, only a formal difficulty of the same kind as that mentioned in Part I in connection with the discussion of the conditions (16), which fix the stationary states of a system consisting of a particle moving in a central field of force. Thus from a simple consideration it will be seen that, in complete analogy to the relations (52) and (53), we get in the present case for the difference between the energy of two slightly different states of the perturbed system, which correspond to the same value of  $I$ ,

$$\delta \mathcal{V} = \nu_1 \delta \mathfrak{J}_1 + \nu_2 \delta \mathfrak{J}_2, \quad (59)$$

where  $\nu_1$  is the frequency with which the shape of the orbit and its position relative to the axis of the field repeats itself at regular intervals and which is characterised by the variation of  $\alpha_2$  and  $\beta_2$ , while  $\nu_2$  is the mean frequency of rotation of the plane of the orbit round this axis characterised by the variation of  $\beta_3$ , and where  $\mathfrak{J}_1$  and  $\mathfrak{J}_2$  are defined by the equations

$$\mathfrak{J}_1 = \int a_2 D\beta_2, \quad \mathfrak{J}_2 = \int_0^{2\pi} a_3 D\beta_3 = 2\pi a_3. \quad (60)$$

In case  $\beta_2$  varies in an oscillating manner with the time, the first integral must be taken over a complete oscillation of this orbital constant, while, if  $\beta_2$  during the perturbations increases or decreases continuously, the integral in the expression for  $\mathfrak{J}_1$  must be taken over an interval of  $2\pi$ , just as the integral in the expression for  $\mathfrak{J}_2$ . By fixing the stationary states of the perturbed system by means of the two conditions<sup>1)</sup>

$$\mathfrak{J}_1 = n_1 h, \quad \mathfrak{J}_2 = n_2 h, \quad (61)$$

where  $n_1$  and  $n_2$  are entire numbers, it will therefore be seen that we obtain the right relation between the additional energy  $\mathfrak{E} = \mathcal{V}$  of the perturbed atom and the fre-

<sup>1)</sup> Quite apart from the problem of perturbed periodic systems, the second of these conditions would also follow directly from certain interesting considerations of EPSTEIN (Ber. d. D. Phys. Ges. XIX, p. 116 (1917)) about the stationary states of systems which allow of what may be called "partial separation of variables". In this case it is possible to choose a set of positional coordinates  $q_1, \dots, q_s$  in such a way that, for some of the coordinates, the conjugated momenta may be considered as functions of the corresponding  $q$ 's only, so that, for these coordinates, quantities  $I$  may be defined by (21) in the same way as for systems for which a complete separation of variables can be obtained. From analogy with the theory of the stationary states of the latter systems, EPSTEIN proposes therefore the assumption, that some of the conditions to be fulfilled in the stationary states of the systems in question may be obtained by putting the  $I$ 's thus defined equal to entire multipla of  $h$ . It will be seen that, in case of systems possessing an axis of symmetry, this leads to the second of the conditions (61), which expresses the condition that in the stationary states the total angular momentum round the axis must be equal to an entire multiple of  $h/2\pi$ . As pointed out in Part I on page 34, this condition would also seem to obtain an independent support from considerations of conservation of angular momentum during a transition between two stationary states.

quencies of the secular perturbations of the orbit of the electron. It will moreover be seen that a state in which the electron moves in a circular orbit perpendicular to the axis of the field, and which beforehand must be expected to belong to the stationary states of the perturbed atom since this orbit will not undergo secular perturbations during a uniform establishment of the external field, will be included among the states determined by (61). In fact, if  $n$  is the number which characterises the corresponding stationary state of the undisturbed system, this state of the perturbed system will correspond to  $n_1 = 0$ ,  $n_2 = n$  or to  $n_1 = n$ ,  $n_2 = n$ , according to whether  $\beta_2$  during the perturbations oscillates between fixed limits, or increases (or decreases) continuously. As regards the application of the conditions (61) it is of importance to point out that, from considerations of the invariance of the a-priori probability of the stationary states of an atomic system during continuous transformations of the external conditions (see Part I, page 9 and 27), it seems necessary to conclude that no stationary state exists corresponding to  $n_2 = 0$ . For this value of  $n_2$  the motion of the electron would take place in a plane through the axis, but for certain external fields such motions cannot be regarded as physically realisable stationary states of the atom, since in the course of the perturbations the electron would collide with the nucleus (compare page 68).

A special case of an external field possessing axial symmetry, in which the secular perturbations are very simple, presents itself if the external forces form a central field with the nucleus at the centre. In this case the solution of the problem of the fixation of the stationary states is given by SOMMERFELD's general theory of central systems, discussed in Part I, which rests upon the fact that these systems allow of separation of variables in polar coordinates. In connection with the above considerations it may be of interest, however, to consider the problem in question directly from the point of view of perturbed periodic systems, because it presents a characteristic example of a degenerate perturbed system. In the present case  $\Psi$  will, besides on  $a_1$ , depend on  $a_2$  only, and from the equations (46) we get therefore the well known result, that the angular momentum of the electron and the plane of its orbit will not vary during the perturbations, and that the only secular effect of the perturbing field will consist in a slow uniform rotation of the direction of the major axis. For the frequency of this rotation we get from (46)

$$v = \frac{1}{2\pi} \frac{D\beta_2}{Dt} = \frac{1}{2\pi} \frac{\partial \Psi}{\partial a_2}, \quad (62)$$

from which we get directly for the difference between the values of  $\Psi$  for two neighbouring states of the perturbed system, for which the corresponding value of  $I$  is the same,

$$\delta \Psi = 2\pi v \delta a_2. \quad (63)$$

This relation, which corresponds to (56), is seen to coincide with (59), since in the present case  $v_2 = 0$  and  $\mathfrak{J}_1 = 2\pi a_2$ . From (63) it follows that the necessary relation between the additional energy of the atom and the frequency of the perturba-

tions is secured if the stationary states in the presence of a small external central field are characterised by the condition

$$\mathfrak{J} = 2\pi a_2 = nh, \quad (64)$$

where  $n$  is an entire number. This condition, which is equivalent with the second of SOMMERFELD's conditions (16), corresponds to (58) and is seen to coincide with the first of the conditions (61), while the second of the latter conditions in the special case under consideration loses its validity corresponding to the fact that the orientation of the plane of the orbit in space is obviously arbitrary. Since, for a Keplerian motion, the major axis of the orbit depends on the total energy only while the minor axis is proportional to the angular momentum, it will be seen from (64) that the presence of a small external field imposes the restriction on the motion of the atom in the stationary states, that the minor axis of the orbit of the electron must be equal to an entire multiple of the  $n^{\text{th}}$  part of the major axis, which was given by  $2a_n$  in (41). This result has been pointed out by SOMMERFELD as a consequence of the application of the conditions (16).

In the preceding it has been shown how it is possible to attack the problem of the stationary states of a perturbed periodic system by an examination of the secular perturbations of the shape and position of the orbit, and to fix these states if the perturbations are of periodic or conditionally periodic type. While these considerations allow to determine the possible values for the total energy of the perturbed system and thereby the frequencies of the components into which the lines of the spectrum of the undisturbed system are split up in the presence of the external field, it is necessary, however, for the discussion of the intensities and polarisations of these components to consider more closely the motion of the particles in the perturbed system and the relation of the total energy of this system to the fundamental frequencies which characterise the motion. In the first place it will be seen that, if the secular perturbations as determined by the equations (46) are of conditionally periodic type, the displacements of the particles of the system in any given direction may, with neglect of small quantities proportional to the intensity of the external forces, be represented, within a time interval sufficiently large for these forces to produce a considerable change in the shape and position of the orbit, as a sum of harmonic vibrations by expressions of the type:

$$\xi = \sum C_{\tau, t_1, \dots, t_{s-1}} \cos 2\pi \{ (\tau \omega_P + t_1 \nu_1 + \dots + t_{s-1} \nu_{s-1}) t + c_{\tau, t_1, \dots, t_{s-1}} \}, \quad (65)$$

where the summation is to be extended over all positive and negative entire values of  $\tau, t_1, \dots, t_{s-1}$ , and where the  $C$ 's and  $c$ 's are two sets of constants, the former of which depend only on the values of the quantities  $\mathfrak{J}_1, \dots, \mathfrak{J}_{s-1}$  defined by (53) and on the value of the quantity  $I$ , which characterises the corresponding state of the undisturbed system which would appear if the external field vanished at a slow and uniform rate. While the quantities  $\nu_1, \dots, \nu_{s-1}$  are the same as those which appear



in the formula (54), and represent the small frequencies of the secular perturbations of the shape and position of the orbit, the quantity  $\omega_P$  may be considered as representing the mean frequency of revolution of the particles in their approximately periodic orbit. As regards the total energy of the perturbed system, it may next be proved that, looking apart from small quantities proportional to the square of the intensity of the external forces, the difference in the total energy in two slightly different states of the perturbed system, for which the values of  $I, \mathfrak{I}_1, \dots, \mathfrak{I}_{s-1}$  differ by  $\delta I, \delta \mathfrak{I}_1, \dots, \delta \mathfrak{I}_{s-1}$  respectively, is given by the relation.<sup>1)</sup>

$$\delta E = \omega_P \delta I + \sum_{k=1}^{s-1} \nu_k \delta \mathfrak{I}_k, \quad (66)$$

which coincides with (52) if  $\delta I = 0$ , and which will be seen to be completely analogous with formula (29) in Part I, holding for an ordinary conditionally periodic system which allows of separation of variables in a fixed set of positional coordinates; just as (65) is analogous to formula (31) representing the displacements of the par-

<sup>1)</sup> From a comparison with formula (8), holding for the energy difference between two neighbouring states of the undisturbed system, and with formula (52), it will be seen that (66) implies the condition  $\omega_P = \omega + \partial \Psi / \partial I$ , where  $\omega$  is the frequency of revolution in the corresponding state of the undisturbed system characterised by the given value of  $I$ , and where, in the partial differential coefficient,  $\Psi$  is considered as a function of  $I$  and  $\mathfrak{I}_1, \dots, \mathfrak{I}_{s-1}$ . This relation can be verified by means of a consideration based on the perturbation equations (44), which takes into account the simple relation between  $\alpha_1$  and  $I$  for the undisturbed system, as well as the relation between the mean rate of variation of  $\beta_1$  with the time and the difference between  $\omega_P$  and  $\omega$ . We shall not enter, however, on the details of the rather intricate calculations involved in such a consideration, since the problems in question allow of a more elegant treatment by means of another analytical method. Thus it will be shown by Mr. H. A. KRAMERS, in the paper mentioned in the end of § 4, that, quite independent of the possibility of separation of variables for the perturbed system in a fixed set of positional coordinates, the theory of secular perturbations exposed in this section offers — if these perturbations as determined by (46) are of conditionally periodic type — a means of disclosing a set of angle variables, which may be used to describe the motion of the perturbed system with the same degree of approximation as that involved in the preceding calculations. According to the definition of angle variables, mentioned in the Note on page 29 in Part I, this means that it is possible, in stead of the positional coordinates  $q_1, \dots, q_s$  of the perturbed system and their conjugated momenta  $p_1, \dots, p_s$ , to introduce a new set of  $s$  variables in such a way, that the  $q$ 's and  $p$ 's are periodic in every of the new variables with period 1, when they are considered as functions of these variables and of their canonically conjugated momenta. These momenta will just coincide with the quantities denoted above by  $I, \mathfrak{I}_1, \dots, \mathfrak{I}_{s-1}$ , and the corresponding angle variables may conveniently be denoted by  $w, w_1, \dots, w_{s-1}$  respectively. Introducing the new variables, the total energy of the perturbed system will be a function of  $I, \mathfrak{I}_1, \dots, \mathfrak{I}_{s-1}$  only, if we look apart from small quantities proportional to  $\lambda^2$ . With this approximation we get consequently by a calculation, analogous to that given in the Note referred to, that the angle variables  $w, w_1, \dots, w_{s-1}$  may be represented as linear functions of the time within an interval of the same order as  $\sigma/\lambda$ . Denoting the rates of variation of  $w, w_1, \dots, w_{s-1}$  by  $\omega_P, \nu_1, \dots, \nu_{s-1}$  respectively, the formulae (65) and (66) are therefore directly obtained, just as the corresponding formulae (31) and (29) in Part I. In this connection it will be observed that, due to the possibility of introduction of angle variables, the conditions (67) appear in the same form as that in which the conditions, which fix the stationary states of ordinary conditionally periodic systems which allow of separation of variables, have been formulated by SCHWARZSCHILD, and which, as mentioned in the Note in Part I, has already been applied by BURGERS to certain systems for which such a separation cannot be obtained.

ticles for such a system. Since moreover, in complete analogy to the conditions (22), the stationary states of the perturbed system are characterised by

$$I = nh, \quad \mathfrak{N}_k = n_k h, \quad (k = 1, \dots, s-1) \quad (67)$$

we see consequently that, for sufficiently small intensity of the external forces, we obtain in the region of large values of  $n$  and of the  $n$ 's a connection between the frequencies of the components of the spectral lines, determined on the quantum theory by means of relation (1), and those to be expected on ordinary electrodynamics, which is of exactly the same type as the analogous connection, discussed in Part I, in case of ordinary conditionally periodic systems which allow of separation of variables. In perfect analogy with the general considerations in Part I, we are therefore led directly to certain simple conclusions as regards the intensities and polarisations of the components into which the lines of the spectrum of the undisturbed periodic system are split up in the presence of the external field. Thus we shall expect that there will exist an intimate connection between the probability of spontaneous transition between two stationary states of the perturbed system, for which  $n = n'$ ,  $n_k = n'_k$  and  $n = n''$ ,  $n_k = n''_k$  respectively, and the values in these states of the coefficient  $C_{\tau, t_1, \dots, t_{s-1}}$  in the expressions for the displacements of the particles, for which  $\tau = n' - n''$  and  $t_k = n'_k - n''_k$ . If for instance, for a certain set of values of  $\tau$  and  $t_1, \dots, t_{s-1}$ , the coefficient  $C_{\tau, t_1, \dots, t_{s-1}}$  in the expressions for the displacements in every direction will be equal to zero for all motions of the perturbed system, we shall expect that the corresponding transitions between two stationary states will be impossible in the presence of the given external field; and if this coefficient is zero for the displacements of the particles in a certain direction only, we shall expect that the corresponding transitions will give rise to the emission of a radiation which is polarised in a plane perpendicular to this direction.

With a characteristic example of these considerations we meet in the case of the spectrum of a hydrogen atom exposed to an external field of force which possesses axial symmetry round an axis through the nucleus. In analogy with the resolution of the motion of an ordinary conditionally periodic system which possesses an axis of symmetry in its constituent harmonic vibrations, discussed in Part I on page 33, it follows from the discussion of the general character of the secular perturbations on page 54 that the motion of the electron in the perturbed atom in this case can be resolved in a number of linear harmonic vibrations parallel to the axis with frequencies  $\tau \omega_p + t_1 \nu_1$  and in a number of circular harmonic rotations perpendicular to the axis with frequencies  $\tau \omega_p + t_1 \nu_1 + \nu_2$ . In complete analogy with the considerations in Part I, we are therefore led to conclude that in the present case only two types of transitions between the stationary states of the perturbed atom are possible. In the transitions of the first type  $n_2$  will remain unaltered and the emitted radiation will give rise to components of the hydrogen lines which will show linear polarisation parallel to the axis. In the transitions of the second type  $n_2$  will change by one unit and the emitted radiation will show circular polarisation when viewed in the direction of the axis. Remembering that, according to



the conditions (61), the angular momentum of the system round the axis in the stationary states is equal to  $n_2 \frac{h}{2\pi}$ , it will be seen moreover that, also in the present case, these conclusions obtain an independent support from a consideration of conservation of angular momentum during the transitions (Compare Part I page 34)<sup>1)</sup>. In the following we will meet with applications of these considerations when discussing the effect of electric and magnetic fields on the hydrogen lines. In the latter case, however, the preceding considerations need some modifications due to the fact, that the external forces acting on the electron cannot be derived from a potential expressed as a function of its positional coordinates; to this point we shall come back in § 5.

Before leaving the general theory of perturbed periodic systems we shall still consider the problem of the effect on the spectrum of a periodic system, undergoing secular perturbations of conditionally periodic type under the influence of a given small external field, if this system is further subject to the influence of a second external field which is small compared with the first field, but the perturbing effect of which is yet large compared with the small effects on the motion, proportional to the square of the intensity of the first perturbing field, which were neglected in the preceding calculations. This problem is closely analogous to the problem, briefly discussed in Part I, of the effect of a small perturbing field on the spectrum of an ordinary conditionally periodic system which allows of separation of variables. As mentioned on page 34, we have in this case, quite independent of the possibility of separation of variables for the perturbed system, that in general the motion under the influence of the external field may still be represented as a sum of harmonic vibrations by a formula of the type (31), if we look apart from small terms proportional to the square of the perturbing forces. Corresponding to this we have in the case under consideration that, independent of the nature of the second external field, the resultant secular perturbations may in general be expressed as a sum of harmonic vibrations of small frequencies of the type (54), if we look apart from small terms of the same order as the product of the secular perturbations produced by the first external field with the square of the ratio between the intensities of the forces due to the first and those due to the second external field. Let us denote this ratio by  $\mu$  and let, as above,  $\lambda$  represent a small constant of the same order as the ratio between the ex-

<sup>1)</sup> Note added during the proof. In an interesting paper by A. RUBINOWICZ (Phys. Zeitschr. XIX, p. 441 and p. 465 (1918)) which has just been published, a similar consideration of conservation of angular momentum has been used to draw conclusions, as regards the possibility of transitions between the stationary states of a conditionally periodic system possessing an axis of symmetry, and as regards the character of the polarisation of the radiation accompanying these transitions. In this way RUBINOWICZ has arrived at several of the results discussed in the present paper; in this connection, however, it may be remarked that, from a consideration of conservation of angular momentum, it is not possible, even for systems possessing axial symmetry, to obtain as complete information, as regards the number and polarisation of the possible components, as from a consideration based on the resolution of the motion of the electron in harmonic vibrations.



ternal forces due to the first field and the internal forces of the system. On the basis of the general relation between energy and frequency in the stationary states, we may then expect that it is possible to fix the motion in these states for the perturbed periodic system in the presence of both external fields with neglect of small terms of the same order as the largest of the quantities  $\mu^2$  and  $\lambda$ , and to fix the corresponding values for the energy with neglect of small terms of the same order as the largest of the quantities  $\lambda\mu^2$  and  $\lambda^2$ .<sup>1)</sup> In general, however, the effect on the spectrum of the perturbed system, produced by the second external field, may be calculated without considering the perturbing effect of this field in detail. In fact, it is in general possible, by means of the principle of the mechanical transformability of the stationary states, with the approximation mentioned to determine the alteration of the energy of the system, due to the presence of the second external field, directly from the character of the secular perturbations produced by the first external field only. Thus let us assume that the second field is slowly established at a uniform rate within a time interval of the same order of magnitude as that in which the system will pass approximately through any state belonging to the cycle of shapes and positions, which the orbit passes through in the stationary states in the presence of the first external field only. Denoting a time interval of this order by  $\vartheta$  and the potential of the first perturbing field by  $\mathcal{Q}$  and that of the second by  $\Delta\mathcal{Q}$ , we get then, by a calculation quite analogous to that given in Part I on page 11 for the alteration in the mean value of the energy of a periodic system during a slow establishment of a small external field, that the alteration in the mean value of  $\alpha_1 + \mathcal{Q}$  taken over a time interval of the same order as  $\vartheta$ , due to the establishment of the second external field, will be a small quantity of the same order of magnitude as  $\vartheta (\Delta\mathcal{Q})^2$ ; but with the notation used above this means, in general, a small quantity of the same order as  $\lambda\mu^2$ . It follows consequently that, with this approximation, the alteration in the energy in a given stationary state, due to the presence of the second perturbing field, is equal to the mean value of the potential of this field taken over the cycle of shapes and positions, which the orbit would pass through in the corresponding stationary state of the perturbed system under the influence of the first external field only. In general, the effect on the spectrum will therefore consist in a small displacement of the original components proportional to the intensity of the forces due to the second perturbing field; and as regards the degree of approximation with which these displacements are defined, it will be seen from the above that, if  $\mu$  is smaller than  $\sqrt{\lambda}$ , the fixation of the energy in the stationary states in the presence of the second external field, and therefore also the determination of the frequencies of the spectral

<sup>1)</sup> In analogy with the considerations on page 50 it may be expected, however, that these limits for the definition of the energy in the stationary states will hold only for the great majority among a large number of atomic systems. Thus in the present case we must be prepared to find that for a small fraction of the systems of the same order as  $\mu^2$  (if  $\mu^2 > \lambda$ ) the energy will differ from that fixed by the method under consideration by small quantities of the same order as  $\mu\lambda$ .

lines by means of (1), allow of the same degree of approximation as the fixation of the energy in the stationary states of the original perturbed periodic system. If  $\mu$  is larger than  $\sqrt{\lambda}$ , however, the stationary states will in general not be as well defined as for the original system, and from relation (1) we may therefore expect that the components will be diffuse, although, as long as  $\mu$  remains small compared with unity, the width of the components will remain small compared with the displacements from their positions in the presence of the first external field alone. Only when  $\mu$  becomes of the same order as unity, the simultaneous effect of both perturbing fields may be expected to consist in a diffusion of the lines of the undisturbed periodic system; unless of course the secular perturbations due to the simultaneous presence of both fields are still of conditionally periodic type, as it may happen in special problems. In certain cases the second external field will not only give rise to small displacements of the original components but also to the appearance of new components of small intensities proportional to  $\mu^2$ . This occurs if for the original perturbed periodic system, due to some peculiarity of the motion, some of the coefficients  $C_{\tau, t_1, \dots, t_{s-1}}$  in the expressions (65) for the displacements of the particles as a sum of harmonic vibrations, corresponding to certain combinations of the numbers  $\tau, t_1, \dots, t_{s-1}$ , are equal to zero, while in the presence of the second external field these coefficients are small quantities proportional to  $\mu$  (Compare Part I, page 34).<sup>1)</sup> In the preceding considerations it has been assumed that the perturbed system in the presence of the first external field is non-degenerate. In case, however, this system is degenerate, it is obviously impossible, by a direct application of the principle of the mechanical transformability of the stationary states, to determine the alteration in the energy in the stationary states of the system, which will be due to the presence of a second external field small compared with the first field; because, as mentioned, the stationary states of the system, in the presence of this field only, will be determined by a number of conditions which is less than the number  $s$  of degrees of freedom, and that consequently the cycles of shapes and positions, which the orbit will pass through in these states, will not be completely determined. For the calculation of the energy in the stationary states it will therefore be necessary to consider the secular perturbing effect of the second external field on these cycles. In the special case where the secular perturbations due to the first field are simply periodic, it will in this way be seen that the problem of the fixation of the stationary states in the presence of the second external field, by means of the method exposed in this section, may be reduced to the problem of the fixation of the stationary states of a system of  $s-2$  degrees of freedom. If, as in the applications considered below,  $s$  is equal to 3, this problem allows of a general solution, and we must therefore expect that in this case the

<sup>1)</sup> As regards the degree of definition with which the positions of the new components will be determined, we must be prepared to find that the frequencies of these components are only defined with neglect of small quantities proportional to  $\lambda\mu$ . Compare the detailed discussion of the example in § 5 on page 97.

effect on the spectrum of the perturbed system produced by an arbitrary second external field, which is small compared with the first, will consist in the splitting up of every component into a number of separate components, just as the effect of an arbitrary small external field on the lines of the spectrum of a simple periodic system of two degrees of freedom. We will meet with applications of the above considerations when considering the effect on the hydrogen spectrum of the combined action of different external fields and when considering the effect of an external field on the spectra of other elements, which latter problem will be discussed in Part III.

### § 3. The fine structure of the hydrogen lines.

An instructive application of the calculations in the last section may be made in connection with the fine structure of the hydrogen lines, which, according to SOMMERFELD's theory mentioned in Part I on page 18, may be explained by taking into account the small variation of the mass of the electron with its velocity, claimed by the theory of relativity. In this connection it must first of all be remarked that all the general considerations in the preceding sections, as regards relations between energy and frequency and as regards the mechanical transformability of the stationary states, hold unaltered if the relativity modifications are taken into account. This follows from the fact that the Hamiltonian equations (4), which are taken as a basis for all the previous calculations, may be used to describe the motion also in this case. If, when the relativity modifications are taken into account, the motion of the system is simply periodic independent of the initial conditions, we shall consequently expect that the stationary states are characterised by the condition  $I = nh$  only, and that the energy and frequency are the same for all states corresponding to a given value of  $n$  in this equation. Further the stationary states will also in the relativity case be fixed by (22), if the system is conditionally periodic and allows of separation of variables; while the stationary states of a perturbed periodic system, also in the relativity case, will be characterised by the conditions (67), if the secular perturbations are of conditionally periodic type.

Now, when the relativity modifications are taken into account, the motion of the particles in the hydrogen atom will not, as assumed in § 1, be exactly periodic, but the orbit of the electron will be of the same type as that, which would appear on ordinary Newtonian mechanics, if the law of attraction between the particles differed slightly from that of the inverse square. If, for the moment, we consider the mass of the nucleus as infinite, the system will allow of a separation of variables in polar coordinates, and the stationary states may consequently be fixed by the conditions (16). In this way SOMMERFELD obtained an expression for the total energy in the stationary states, which, with neglect of small quantities of higher order than the



square of the ratio of the velocity of the electron and the velocity of light  $c$ , is given by<sup>1)</sup>

$$E = -\frac{2\pi^2 N^2 e^4 m}{h^2 (n_1 + n_2)^2} \left[ 1 + \frac{\pi^2 N^2 e^4}{c^2 h^2 (n_1 + n_2)^2} \left( 1 + 4 \frac{n_1}{n_2} \right) \right], \quad (68)$$

where, as in the calculations in § 1, the charge and the mass of the electron are denoted by  $-e$  and  $m$ , and for sake of generality the charge of the nucleus by  $Ne$ . Further  $n_1$  and  $n_2$  are the integers appearing on the right side of the conditions (16) as factors to PLANCK'S constant. While  $n_1$  may take the values 0, 1, 2, ..., it will be seen that  $n_2$  can only take the values 1, 2, ..., because in the present case there will obviously not correspond any stationary state to  $n_2 = 0$ , since in such a state the electron would collide with the nucleus. Introducing the experimental values for  $e$ ,  $h$  and  $c$ , it is found that  $e^2/hc$  is a small quantity of the same order as  $10^{-3}$ ; and, unless  $N$  is large number, the second term within the bracket on the right side of (68) will consequently be very small compared with unity. Putting  $n_1 + n_2 = n$ , it will further be seen that the factor outside the bracket will coincide with the expression for  $W_n$  given by (41) in § 1, if we look apart from the small correction due to the finite mass of the nucleus. Due to the presence of the second term within the bracket, we thus see that, for any value of  $n$ , formula (68) gives a set of values for  $E$  which differ slightly from each other and from  $-W_n$ . SOMMERFELD'S theory leads therefore to a direct explanation of the fact, that the hydrogen lines, when observed by instruments of high dispersive power, are split up in a number of components situated closely to each other; and, by means of formula (68) in connection with relation (1), it was actually found possible, within the limits of experimental errors, to account for the frequencies of the components of this so-called fine structure of the hydrogen lines. Moreover the theory was supported in the most striking way by PASCHEN'S<sup>2)</sup> recent investigation of the fine structure of the lines of the analogous helium spectrum, the frequencies of which are represented approximately by formula (35), if in the expression for  $K$ , given by (40), we put  $N = 2$ . As it should be expected from (68), the components of these lines were found to show frequency differences several times larger than those of the hydrogen lines, and from his measurements PASCHEN concluded, that it was possible on SOMMERFELD'S theory to account completely for the frequencies of all the components observed.

We shall not enter here on the details of the calculation leading to (68), but shall only show how this formula may be simply interpreted from the point of

<sup>1)</sup> A. SOMMERFELD, Ann. d. Phys. LI, p. 53 (1916). Compare also P. DEBYE, Phys. Zeitschr., XVII, p. 512 (1916). In the special case of circular orbits ( $n_1 = 0$ ), this expression coincides with an expression previously deduced by the writer (Phil. Mag. XXIX p. 332 (1915)), by a direct application of the condition  $I = nh$  to these periodic motions.

<sup>2)</sup> F. PASCHEN, Ann. d. Phys. L, p. 901 (1916). See also E. J. EVANS and C. CROXSON, Nature, XCVII, p. 56 (1916).

view of perturbed periodic systems. Thus, by a simple application of relativistic mechanics, it is found that, if the equation of a Keplerian ellipse in polar coordinates is given by  $r = f(\vartheta)$ , the equation of the orbit of the electron in the case under consideration will be given by  $r = f(\gamma\vartheta)$  where  $\gamma$  is a constant given by  $\gamma^2 = 1 - \left(\frac{Ne^2}{pc}\right)^2$ , in which expression  $p$  denotes the angular momentum of the electron round the nucleus.<sup>1)</sup> Now in the stationary states the quantity in the bracket, which is of the same order of magnitude as the ratio between the velocity of the electron and the velocity of light, will be very small, unless  $N$  is a large number, and it will therefore be seen that the orbit of the electron can be described as a periodic orbit on which a slow uniform rotation is superposed. Denoting the frequency of revolution in the periodic orbit by  $\omega$  and the frequency of the superposed rotation by  $\nu_R$ , we have, with neglect of small quantities of higher order than the square of the ratio between the velocity of the electron and the velocity of light,

$$\nu_R = \omega(1-\gamma) = \frac{1}{2} \omega \left(\frac{Ne^2}{pc}\right)^2. \quad (69)$$

Comparing this formula with equation (62) and remembering that, with the approximation in question,  $p$  may be replaced by the quantity denoted in § 2 by  $a_2$ , we see that the frequency of the secular rotation of the orbit will be the same as that which would appear, if the variation of the mass of the electron was neglected, but if the atom was subject to a small external central force the mean value of the potential of which, taken over a revolution of the electron, was equal to

$$\psi = -\omega \frac{\pi N^2 e^4}{c^3 a_2}. \quad (70)$$

This is simply shown, however, to be equal to the expression for  $\psi$  corresponding to a small attractive force varying as the inverse cube of the distance. In fact, let the potential of such a force be given by  $\mathcal{Q} = C/r^2$ , where  $C$  is a constant and  $r$  the length of the radius vector from the nucleus to the electron. By means of the relation  $a_2 = mr^2\dot{\vartheta}$ , where  $\vartheta$  is the angular distance of the radius vector from a fixed line in the plane of the orbit, we get then

$$\psi = \frac{1}{\sigma} \int_0^\sigma \frac{C}{r^2} dt = \frac{\omega m C}{a_2} \int_0^{2\pi} d\vartheta = \frac{2\pi \omega m C}{a_2},$$

which expression is seen to coincide with (70), if  $C = -\frac{N^2 e^4}{2c^3 m}$ .

If the relativity modifications are taken into account, and if for a moment we would imagine that the nucleus, in addition to its usual attraction, exerted

<sup>1)</sup> See f. inst. A. SOMMERFELD, loc. cit. p. 47.

a small repulsion on the electron, proportional to the inverse cube of the distance and equal and opposite to the attraction just mentioned, we would therefore obtain a system for which, with neglect of small quantities of higher order than the square of the ratio between the velocity of the electron and the velocity of light, every orbit would be periodic independent of the initial conditions, and for which consequently the stationary states would be fixed by the single condition  $I = nh$ . Now the actual hydrogen atom may obviously be considered as a perturbed system, formed by this periodic system, when it is exposed to a small central field for which the value of  $\mathcal{V}$  is given by (70). With the approximation mentioned, we get therefore for the total energy in the stationary states of the atom

$$E = E'_n - \frac{8\pi^4 N^4 e^8 m}{h^4 c^2} \frac{1}{n^3 \pi}, \quad (71)$$

where  $E'_n$  is the energy in the stationary states of the periodic system just mentioned, and where the last term is obtained by introducing in (70) the value of  $u_2$  given by (64) and the value of  $\omega_n$  given by (41), neglecting the small correction due to the finite mass of the nucleus. Remembering that in our notation  $n_1 + n_2 = n$  and  $n_2 = n$ , it will be seen that, as regards the small differences in the energy of the different stationary states corresponding to the same value of  $n$ , formula (71) gives the same result as SOMMERFELD's formula (68). In fact, comparing (68) and (71), we get

$$E'_n = - \frac{2\pi^2 N^2 e^4 m}{h^2 n^2} \left( 1 - \frac{3\pi^2 N^2 e^4}{c^2 h^2 n^2} \right), \quad (72)$$

which is seen to be a function of  $n$  only. This expression might also have been deduced directly from the condition  $I = nh$  by considering, for instance, a circular orbit, in which case the calculation can be very simply performed.

In connection with the above calculations, it may be remembered that the fixation of the stationary states, leading to the formulæ (68) or (71), is based on the assumption, that the motion of the electron can be determined as that of a mass point which moves in a conservative field of force, according to the laws of ordinary relativistic mechanics, and that we have looked apart from all such forces which, according to the ordinary theory of electrodynamics, would act on an accelerated charged particle, and which constitute the reaction from the radiation which on this theory would accompany the motion of the electron. Some procedure of this kind, which means a radical departure from the ordinary theory of electrodynamics, is obviously necessary in the quantum theory in order to avoid dissipation of energy in the stationary states. Since we are entirely ignorant as regards the mechanism of radiation, we must be prepared, however, to find that the above treatment will allow to determine the motion in the stationary states, only with an approximation which looks apart from small quantities of the same order as the ratio between the radiation forces in ordinary electrodynamics and the main forces on the electron



due to the attraction from the nucleus.<sup>1)</sup> Now it is easily shown that this ratio will be a small quantity of the same order of magnitude as  $N^2 \left( \frac{e^2}{pc} \right)^3$ , and it would therefore beforehand seem justified in the expression for the total energy in the stationary states to retain small terms of the same order as the second term in (71), while at the same time it might appear highly questionable, whether, in the complete expression for the total energy in the stationary states deduced by SOMMERFELD and DEBYE on the basis of the conditions (16), it has a physical meaning to retain terms of higher order than those retained in formula (68); unless  $N$  is a large number, as in the theory of the Röntgenspectra to be discussed in Part III.

While the preceding considerations, which deal with the determination of the energy in the stationary states of the hydrogen atom, allow to determine the frequency of the radiation which would be emitted during a transition between two such states, they leave quite untouched the problem of the actual occurrence of these transitions in the luminous gas, and therefore give no direct information about the number and relative intensities of the components into which the hydrogen lines may be expected to split up as a consequence of the relativity modifications. This problem has recently been discussed by SOMMERFELD<sup>2)</sup>, who in this connection emphasises the importance of the different a-priori probabilities of the stationary states, characterised by different sets of values of the  $n$ 's in the conditions (16). Thus SOMMERFELD attempts to obtain a measure for the relative intensities of the components of the fine structure of a given line, by comparing the intensities observed with the products of the values of the a-priori probabilities of the two states, involved in the emission of the components under consideration; and he tries in this connection to test different expressions for these a-priori probabilities (See Part I, pag. 26). In this way, however, it was not found possible to account in a satisfactory manner for the observations; and the difficulty in obtaining an explanation of the intensities on this basis was also strikingly brought out by the fact, that the number and relative intensities of the components observed varied in a remarkable way with the experimental conditions under which the lines were

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<sup>1)</sup> Compare Part I, p. 6. It may in this connection be noted that the degree of approximation, involved in the determination of the frequencies of an atomic system by means of relation (1) if in the fixation of the stationary states we look apart from small forces of the same order of magnitude as the radiation forces in ordinary electrodynamics, would appear to be intimately connected with the limit of sharpness of the spectral lines, which depends on the total number of waves contained in the radiation emitted during the transition between two stationary states. In fact, from a consideration based on the general connection between the quantum theory and the ordinary theory of radiation, it seems natural to assume that the rate, at which radiation is emitted during a transition between two stationary states, is of the same order of magnitude as the rate, at which radiation would be emitted from the system in these states according to ordinary electrodynamics. But this will be seen to imply that the total number of waves in question will just be of the same order as the ratio between the main forces acting on the particles of the system and the reaction from the radiation in ordinary electrodynamics.

<sup>2)</sup> A. SOMMERFELD, Ber. Akad. München, 1917, p. 83.

excited. Thus PASCHEN found a greater number of components in the fine structure of the helium lines, mentioned above, when the gas was subject to a condensed interrupted discharge, than when a continuous voltage was applied. It would seem, however, that all the facts observed obtain a simple interpretation on the basis of the general considerations about the relation between the quantum theory of line spectra and the ordinary theory of radiation discussed in Part I. According to this relation, we shall assume that the probability, for a transition between two given stationary states to take place, will depend not only on the a-priori probability of these states, which is determining for their occurrence in a distribution of statistical equilibrium, but will also depend essentially on the motion of the particles in these states, characterised by the harmonic vibrations in which this motion can be resolved. Now, in the absence of external forces, the motion of the electron in the hydrogen atom forms a special simple case of the motion of a conditionally periodic system possessing an axis of symmetry, and may therefore be represented by trigonometric series of the type deduced for such motions in Part I. Taking a line through the nucleus perpendicular to the plane of the orbit as  $z$ -axis, we get from the calculations on page 32

$$z = \text{const.}$$

and

$$x = \sum C_\tau \cos 2\pi \{ (\tau\omega_1 + \omega_2)t + c_\tau \}, \quad \pm y = \sum C_\tau \sin 2\pi \{ (\tau\omega_1 + \omega_2)t + c_\tau \}, \quad (73)$$

where  $\omega_1$  is the frequency of the radial motion and  $\omega_2$  is the mean frequency of revolution, and where the summation is to be extended over all positive and negative entire values of  $\tau$ . It will thus be seen that the motion may be considered as a superposition of a number of circular harmonic vibrations, for which the direction of rotation is the same as, or the opposite of, that of the revolution of the electron round the nucleus, according as the expression  $\tau\omega_1 + \omega_2$  is positive or negative respectively. From the relation just mentioned between the quantum theory of line spectra and the ordinary theory of radiation, we shall therefore in the present case expect that, if the atom is not disturbed by external forces, only such transitions between stationary states will be possible, in which the plane of the orbit remains unaltered, and in which the number  $n_2$  in the conditions (16) decreases or increases by one unit; i. e. where the angular momentum of the electron round the nucleus decreases or increases by  $h/2\pi$ . From the relation under consideration, we shall further expect that there will be an intimate connection between the probability of a spontaneous transition of this type between two stationary states, for which  $n_1$  is equal to  $n'_1$  and  $n''_1$  respectively, and the intensity of the radiation of frequency  $(n'_1 - n''_1)\omega_1 \pm \omega_2$ , which on ordinary electrodynamics would be emitted by the atom in these states, and which would depend on the value  $C_\tau$  of the amplitude of the harmonic rotation, corresponding to  $\tau = \pm(n'_1 - n''_1)$ , which appears in the motion of the electron. Without entering upon a closer examination of the numerical values of these amplitudes, it will directly be seen that the amplitudes of the harmonic rotations, which have the same direction as the revolution of the electron,

in general, are considerably larger than the amplitudes of the rotations in the opposite direction, and we shall accordingly expect that the probability of spontaneous transition will in general be much larger for transitions, in which the angular momentum decreases, than for transitions in which it increases. This expectation is verified by PASCHEN's observations of the fine structure of the helium lines, which show that, for a given line, the components corresponding to the transitions of the former kind are by far the strongest. On PASCHEN's photographs, however, especially in the case of the application of a condensed discharge to the vacuum tube containing the gas, there appear, in addition to the main components corresponding to transitions for which the angular momentum changes by  $h/2\pi$ , a number of weaker components, corresponding to transitions for which the angular momentum remains unchanged or changes by higher multiples of  $h/2\pi$ . This fact obtains a simple interpretation on the considerations in Part I on page 34 about the influence of small external forces on the spectrum of a conditionally periodic system. Thus, in the presence of small perturbing forces, the motion will generally not remain in a plane, and in the trigonometric series representing the displacement of the electron in space, there will occur small terms corresponding to frequencies  $(\tau_1 \omega_1 + \tau_2 \omega_2)$ , where  $\tau_2$  may be different from one. In the presence of such forces, we shall therefore expect that, in addition to the regular probabilities of the above mentioned main transitions, there will appear small probabilities for other transitions.<sup>1)</sup> A detailed discussion of these problems will be given in a later paper by Mr. H. A. KRAMERS, who on my proposal has kindly undertaken to examine the resolution of the motion of the electron in its constituent harmonic vibrations more closely, and who has deduced explicit expressions for the amplitudes of these vibrations, not only for the motion of the electron in the undisturbed atom, but also for the perturbed motion in the presence of a small external homogeneous electric field. As it will be shown by KRAMERS, these calculations allow to account in particulars for the observations of the relative intensities of the components of the fine structure of the hydrogen lines and the analogous helium lines, as well as for the characteristic way in which this phenomenon is influenced by the variation of the experimental conditions.

#### § 4. The effect of an external electric field on the hydrogen lines.

As mentioned in the introduction, a detailed theory of the characteristic effect of an external homogeneous electric field on the hydrogen spectrum, discovered by

<sup>1)</sup> Note added during the proof. As remarked in Part I, this consideration obtains a striking confirmation by the observation of the appearance of new series of lines in the ordinary series spectra of helium and other elements, when the atoms are exposed to an intense external electric field. As it will be discussed more closely in Part III, it is possible in this way to account in detail for the manifold results, regarding the appearance of such series in the helium spectrum, which have been published quite recently by J. STARK (Ann. d. Phys. LVI, p. 577 (1918)) and by G. LIEBERT (ibid. LVI, p. 589 and p. 610 (1918)).



STARK, has been given by EPSTEIN and SCHWARZSCHILD on the basis of the general theory of conditionally periodic systems which allow of separation of variables. Before we enter on the discussion of the results of the calculations of these authors, we shall first, however, show how the problem may be treated in a simple way by means of the considerations about perturbed periodic systems, developed in § 2.

Consider an electron of mass  $m$  and charge  $-e$ , rotating round a positive nucleus of infinite mass and of charge  $Ne$ , and subject to a homogeneous electric field of intensity  $F$ , and let us for the present neglect the small effect of the relativity modifications. Using rectangular coordinates, and taking the nucleus as origin and the  $z$ -axis parallel to the external field, we get for the potential of the system relative to the external field, omitting an arbitrary constant,

$$\Omega = eFz.$$

Calculating now the mean value of  $\Omega$  over a period  $\sigma$  of the undisturbed motion, we see at once, from considerations of symmetry, that this mean value  $\Psi$  will depend only on the component of the external electric force in the direction of the major axis of the orbit. We have therefore

$$\Psi = eF \cos \varphi \frac{1}{\sigma} \int_0^\sigma r \cos \vartheta dt,$$

where  $\varphi$  is the angle between the  $z$ -axis and the major axis, taken in the direction from the nucleus to the aphelium, and where  $r$  is the length of the radius-vector from the nucleus to the electron, and  $\vartheta$  the angle between this radius-vector and the major axis. By means of the well known equations for a Keplerian motion

$$r \cos \vartheta = a (\cos u + \varepsilon), \quad \frac{dt}{\sigma} = (1 + \varepsilon \cos u) \frac{du}{2\pi},$$

where  $2a$  is the major axis,  $\varepsilon$  the eccentricity and  $u$  the so-called eccentric anomaly, this gives

$$\Psi = eF \cos \varphi \frac{1}{2\pi} \int_0^{2\pi} a (\cos u + \varepsilon) (1 + \varepsilon \cos u) du = \frac{3}{2} \varepsilon a e F \cos \varphi. \quad (74)$$

We see thus that  $\Psi$  is equal to the potential energy relative to the external field, which the system would possess, if the electron was placed at a point, situated on the major axis of the ellipse and dividing the distance  $2\varepsilon a$  between the foci in the ratio 3:1. This point may be denoted as the "electrical centre" of the orbit. From the approximate constancy of  $\Psi$  during the motion, proved in § 2, it follows therefore in the first place that, with neglect of small quantities of the same order of magnitude as the ratio between the external force and the attraction from the nucleus, the electrical centre will during the perturbations of the orbit remain in a fixed plane perpendicular to the direction of the external force. From the considerations in § 2 it follows further, that the total

energy in the stationary states of the system in the presence of the field, with neglect of small quantities proportional to  $F^2$ , will be equal to  $E_n \pm \mathcal{U}$ , where  $E_n$  is the energy of the hydrogen atom in its undisturbed stationary state. Since both  $\varepsilon$  and  $\cos \varphi$  are numerically smaller than one, we obtain therefore at once from (74) a lower and an upper limit for the possible variations of the energy in the stationary states, due to the field. Introducing from (41) the values of  $E_n$  and  $a_n$ , and neglecting, here as well as in the following calculations in this section, the small correction due to the finite mass of the nucleus — not only in the expression for the additional energy but, for the sake of brevity, also in the main term — we get for these limits

$$E = -\frac{2\pi^2 N^2 e^4 m}{h^3 n^2} \pm \frac{3h^2 n^2}{8\pi^2 N e m} F, \quad (75)$$

which formula coincides with the expression previously deduced by the writer by applying the condition  $I = nh$  to the two (physically not realisable) limiting cases, corresponding to  $\varepsilon = 1$  and  $\cos \varphi = \pm 1$ , in which the orbit remains periodic in the presence of the field.<sup>1)</sup>

In order to obtain further information as to the values of the energy in the stationary states in the presence of the field, it is necessary to consider more closely the variation of the orbit during the perturbations. Since the external forces possess axial symmetry, the problem of the stationary states might be treated by means of the procedure indicated in § 2 on page 55. In the present special case, however, the stationary states of the atom may be very simply determined, due to the fact that the secular perturbations are simply periodic independent of the initial shape and position of the orbit, so that we are concerned with a degenerate case of a perturbed periodic system. This property of the perturbations follows already from some calculations given by SCHWARZSCHILD<sup>2)</sup> in a previous attempt to explain the STARK effect of the hydrogen lines, without the help of the quantum theory, by means of a direct consideration of the harmonic vibrations into which the motion may be resolved, according to the analytical theory of conditionally periodic systems. Starting from the above result, that the electrical centre moves in a plane perpendicular to the direction of the external field, the periodicity of the perturbations may also be proved in the following way, by means of a simple consideration of the variation of the angular momentum of the electron round the nucleus, due to the effect of the external electric force.

Using again rectangular coordinates with the nucleus at the origin and the  $z$ -axis parallel to the direction of the electric force, and calling the coordinates of the electrical centre  $\xi, \eta, \zeta$ , we have according to formula (74)

<sup>1)</sup> See N. BOHR, Phil. Mag. XXVII, p. 506 (1914) and XXX, p. 394 (1915). Compare also E. WARBURG, Verh. d. D. Phys. Ges. XV, p. 1259 (1913), where it was pointed out, for the first time, that the effect of an electric field on the hydrogen lines to be expected on the quantum theory was of the same order of magnitude as the effect observed by STARK.

<sup>2)</sup> K. SCHWARZSCHILD, Verh. d. D. Phys. Ges. XVI, p. 20 (1914).

$$\xi^2 + \eta^2 + \zeta^2 = \left(\frac{3}{2} \varepsilon a\right)^2, \quad \zeta = \text{const.} \quad (1^*)$$

Denoting the components parallel to the  $x$ ,  $y$  and  $z$ -axis of the angular momentum of the electron round the nucleus, considered as a vector, by  $P_x$ ,  $P_y$  and  $P_z$ , we have next

$$P_x^2 + P_y^2 + P_z^2 = (1 - \varepsilon^2)(2\pi m a^2 \omega)^2, \quad P_z = \text{const.} \quad (2^*)$$

Since the angular momentum is perpendicular to the plane of the orbit, we have further

$$\xi P_x + \eta P_y + \zeta P_z = 0. \quad (3^*)$$

Now we have for the mean values of the rates of variation of  $P_x$  and  $P_y$  with the time

$$\frac{DP_x}{Dt} = eF\eta, \quad \frac{DP_y}{Dt} = -eF\xi. \quad (4^*)$$

From this we get, differentiating (1\*) and (2\*) with respect to the time, and remembering that  $a$  and  $\omega$  remain constant during the perturbations,

$$\xi \frac{D\xi}{Dt} + \eta \frac{D\eta}{Dt} = -K^2 \left( P_x \frac{DP_x}{Dt} + P_y \frac{DP_y}{Dt} \right) = -eFK^2(\eta P_x - \xi P_y), \quad (5^*)$$

where

$$K = \frac{3}{4\pi m a \omega}. \quad (6^*)$$

On the other hand we have, differentiating (3\*) and introducing (4\*),

$$P_x \frac{D\xi}{Dt} + P_y \frac{D\eta}{Dt} = 0,$$

which together with (5\*) gives

$$\frac{D\xi}{Dt} = eFK^2 P_y, \quad \frac{D\eta}{Dt} = -eFK^2 P_x,$$

from which we get, by means of (4\*),

$$\frac{D^2\xi}{Dt^2} = -e^2 F^2 K^2 \xi, \quad \frac{D^2\eta}{Dt^2} = -e^2 F^2 K^2 \eta,$$

the solution of which is

$$\xi = \mathfrak{A} \cos 2\pi(\mathfrak{o}t + \mathfrak{a}), \quad \eta = \mathfrak{B} \cos 2\pi(\mathfrak{o}t + \mathfrak{b}), \quad (7^*)$$

where  $\mathfrak{A}$ ,  $\mathfrak{a}$ ,  $\mathfrak{B}$  and  $\mathfrak{b}$  are constants, and where, introducing (6\*), we have

$$\mathfrak{o} = \frac{eF_0K}{2\pi} = \frac{3eF}{8\pi^2 m a \omega}. \quad (8^*)$$

During the perturbations the electrical centre will thus perform slow harmonic vibrations perpendicular to the direction of the electric force, with a frequency which is proportional to the intensity of the electric field, but, for a given value of  $F$ , quite independent of the initial shape of the orbit and its position relative to the direction of the field. For the value of this frequency in the multitude of states of the perturbed system, for which the mean value of the inner energy is equal to the energy  $E_n$  in a stationary state of the undisturbed system corresponding to a given value of  $n$ , we get from the above calculation, introducing for  $a$  and  $\omega$  the values of  $a_n$  and  $\omega_n$  given by (41),



$$\nu_F = \frac{3hn}{8\pi^2 N e m} F. \quad (76)$$

Now from the periodic motion of the electrical centre we may conclude that, in the presence of the field, the system will be able to emit or absorb a radiation of frequency  $\nu_F$ , and that accordingly the possible values of the additional energy of the system in the presence of the field will be given directly by PLANCK's fundamental formula (9), holding for the possible values of the total energy of a linear harmonic vibrator, if in this formula  $\omega$  is replaced by the above frequency  $\nu_F$ . Since further a circular orbit, perpendicular to the direction of the electric force, will not undergo secular perturbations during a slow establishment of the field, and therefore must be included among the stationary states of the perturbed system, we get for the total energy of the atom in the presence of the field

$$E = E_n + n\nu_F h = -\frac{2\pi^2 N^2 e^4 m}{n^2 h^2} + \frac{3h^2 n n}{8\pi^2 N e m} F, \quad (77)$$

where  $n$  is an entire number which in the present case may be taken positive as well as negative. From a comparison between (75) and (77), we see that the presence of the external field imposes the restriction on the motion of the atom in the stationary states, that the plane in which the electrical centre of the orbit moves must have a distance from the nucleus equal to an entire multiple of the  $n^{\text{th}}$  part of its maximum distance  $\frac{3}{2} a_n$ .

The result, contained in formula (77), is in agreement with the expression for the total energy in the stationary states, deduced by EPSTEIN and SCHWARZSCHILD by means of the general theory of conditionally periodic systems based on the conditions (22). The treatment of these authors rests upon the fact, that, as mentioned in Part I, the equations of motion for the electron in the present problem may be solved by means of separation of variables in parabolic coordinates (compare page 21). Taking for  $q_1$  and  $q_2$  the parameters of the two paraboloids of revolution, which pass through the instantaneous position of the electron and which have their foci at the nucleus and their axes parallel to the direction of the field, and for  $q_3$  the angular distance between the plane through the electron and the axis of the system and a fixed plane through this axis, the momenta  $p_1, p_2, p_3$  will during the motion depend on the corresponding  $q$ 's only, and the stationary states will be fixed by three conditions of the type (22). With neglect of small quantities proportional to higher powers of  $F$ , the final formula for the total energy, obtained by EPSTEIN in this way, is given by

$$E = -\frac{2\pi^2 N^2 e^4 m}{h^2 (n_1 + n_2 + n_3)^2} - \frac{3h^2 (n_1 + n_2 + n_3)(n_1 - n_2)}{8\pi^2 N e m} F, \quad (78)$$

<sup>1)</sup> P. EPSTEIN, Ann. d. Phys. L, p. 508 (1916).

where  $n_1, n_2, n_3$  are the positive entire numbers which occur as factors to PLANCK's constant on the right sides of the mentioned three conditions.

As regards the possible values of the total energy of the hydrogen atom in the presence of the electric field, it will be seen that (78) coincides with (77) if we put  $n_1 + n_2 + n_3 = n$  and  $n_2 - n_1 = n$ . At the same time it will be observed, however, that the motion in the stationary states, as fixed by the procedure followed by EPSTEIN, is more restricted than was necessary in order to secure the right relation between the additional energy and the frequency of the secular perturbations. Thus, in addition to the condition which fixes the plane in which the electrical centre moves, EPSTEIN's theory involves the further condition, that the angular momentum of the electron round the axis of the perturbed system is equal to an entire multiple of  $h/2\pi$ : which multiple is seen to be even or uneven, according as  $n + n$  is an even or an uneven number respectively. This circumstance is intimately connected with the fact that, although the perturbed system under consideration is degenerate if we look apart from small quantities proportional to the square of the intensity of the external force, the degenerate character of the system does not reveal itself from the point of view of the theory of stationary states based on the conditions (22), because the system under consideration allows of separation of variables only in one set of positional coordinates. On the other hand, this degenerate character of the system has been emphasised by SCHWARZSCHILD<sup>1)</sup> on the basis of the theory of stationary states based on the introduction of angle variables, in which the periodicity properties of the motion play an essential part. In a later discussion of this point EPSTEIN<sup>2)</sup> calls attention to the fact that, if small quantities proportional to the square of the electric force are taken into account, the system appears no more as degenerate; and he finds therein a justification of the fixation of the stationary states by means of (22). From the point of view of perturbed systems, this would mean that the motion in the stationary states of the system in question, as fixed by (22), would certainly be stable for infinitely small disturbances, but that we should expect finite deviations from the motion in these states, already if the system was exposed to a second perturbing field, the intensity of which was only of the same order as the product of the external electric force with the ratio between this force and the attraction from the nucleus. A closer consideration, however, in which regard is taken to the influence of the relativity modifications, learns that the degree of stability of the motion in the stationary states, as determined by (22), actually is often much higher, the order of magnitude of the external force, necessary to cause finite deviations from this motion, being of the same order as the product of the attraction from the nucleus with the square of the ratio of the velocity of the electron and the velocity of light. To this point we shall come back at the end of this section, when considering the simultaneous perturbing influence on the

<sup>1)</sup> K. SCHWARZSCHILD, Ber. Akad. Berlin, 1916, p. 548.

<sup>2)</sup> P. EPSTEIN, Ann. d. Phys. LI, p. 168 (1916).

motion of the electron in the hydrogen atom, due to the relativity modifications and an external electric field.

In the deduction of formula (78) there is looked apart, not only from the effect on the motion of the electron due to the small modifications in the laws of mechanics claimed by the theory of relativity, but also from the effect of possible forces which might act on the electron, corresponding to the reaction from the radiation in ordinary electrodynamics. If, however, for the moment we exclude all stationary states for which the angular momentum round the axis of the system would be equal to zero ( $n_3 = 0$ ), the total angular momentum of the electron round the nucleus will during the perturbations always remain larger than or equal to  $h/2\pi$ , just as in the stationary states considered in the theory of the fine structure; and, according to the considerations on page 66, we shall therefore expect that the effect of the neglect of possible "radiation" forces will be small compared with the effect of the relativity modifications. On the other hand, if the intensity of the electric field is of the same order of magnitude as that applied in STARK's experiments, the effect of these modifications must again be expected to be very small compared with the total effect of the electric force on the hydrogen lines, since the perturbing effect of this force on the Keplerian motion of the electron will be very large compared with the corresponding effects of the relativity modifications. If, on the contrary, we would consider a state of the atom for which  $n_3$  was equal to zero, the orbit would be plane and would during the perturbations assume shapes, for which the total angular momentum round the nucleus was very small, and in which the electron during the revolution would pass within a very short distance from the nucleus. In such a state the effect of the relativity modifications on the motion of the electron would be considerable, but quite apart from this a rough calculation shows that the amount of energy, which, on ordinary electrodynamics, would be emitted during the intervals in which the angular momentum during the perturbations of the orbit remains small, is so large that it would hardly seem justifiable to calculate the motion and the energy in these states by neglecting all forces corresponding to the radiation forces in ordinary electrodynamics. We need not, however, enter more closely on these difficulties, because, on the general considerations in Part I about the a-priori probability of the different stationary states, we are forced to conclude that, for any value of the external electric field, no state which would correspond to  $n_3 = 0$  will be physically possible; since any such state might be transformed continuously, and without passing through a degenerate system, into a state which obviously cannot represent a physically realisable stationary state (compare pag. 27). In fact, if we imagine that an external central field of force, varying as the inverse cube of the distance from the nucleus, is slowly established, it would be possible to compensate the secular effect of the relativity modifications and to obtain orbits in which the electron would pass within any given, however small, distance from the nucleus. As regards the other stationary states fixed



by (22), which correspond to  $n_3 \geq 1$ , we shall according to the considerations in Part I expect that their a-priori probabilities are all equal.<sup>1)</sup>

As regards the comparison between the theory and the experiments, it will be remembered that STARK found that every hydrogen line in the presence of an electric field was split up in a number of polarised components, in a way different for the different lines. When viewed parallel to the direction of the field, there appeared a number of components polarised parallel to the field and a number of components polarised perpendicular to the field; when viewed in the direction of the field, only the latter components appeared, but without showing characteristic polarisation. Apart from the marked symmetry of the resolution of every line, the distances between successive components and their relative intensities varied in an apparently irregular way from component to component. As pointed out by EPSTEIN and SCHWARZSCHILD, however, it is possible by means of (78), in connection with relation (1), to account in a convincing way for STARK's measurements as regards the frequencies of the components. Especially a closer examination of these measurements showed that all the differences between the frequencies of the components were equal to entire multipla of a certain quantity, which was the same for all lines in the spectrum and, within the limits of experimental errors, equal to the theoretical value  $\frac{3hF}{8\pi^2Nem}$ . On the other hand, the theories of EPSTEIN and SCHWARZSCHILD gave no direct information as regards the question of the polarisation and intensity of the different components. Comparing formula (78) with STARK's observations, EPSTEIN pointed out, however, that the polarisation of the different components observed could apparently be accounted for by the rule: that a transition between two stationary states gives rise to a component polarised parallel to the field, if  $n_3$  remains unchanged or is changed by an even number of units; while a component, corresponding to a transition in which  $n_3$  is changed by an uneven number of units,

<sup>1)</sup> By a simple enumeration it follows from this result, that the total number of different stationary states of the hydrogen atom, subject to a small homogeneous electric field, which corresponds to a stationary states of the undisturbed atom, characterised by a given value of  $n$  in the condition  $I = nh$ , is equal to  $n(n+1)$ . This expression is directly obtained, if we remember that  $n = n_1 + n_2 + n_3$  and if we count each state, characterised by a given combination of the positive integers  $n_1, n_2, n_3$ , as double, corresponding to the two possible opposite directions of rotation of the electron round the axis of the field. With reference to the necessary stability for a small variation of the external conditions of the statistical distribution of the values of the energy among a large number of atoms in temperature equilibrium (see Note on page 43), it will be seen that the expression  $n(n+1)$  may be taken as a measure for the relative value of the a-priori probability of the different stationary states of the undisturbed hydrogen atom, corresponding to different values of  $n$ . The problem of the determination of this a-priori probability has been discussed by K. HERZFELD (Ann. d. Phys. LI, p. 261 (1916)) who, by an examination of the volumes of the different extensions in the phase space which might be considered as belonging to the different stationary states of the hydrogen atom, has arrived at an expression for the a-priori probability of these states which differs from the above. From the point of view, as regards the principles of the quantum theory, taken in the present paper, a consideration of this kind, however, does not, as explained in Part I on page 26, afford a rational means of determining the a-priori probability of the stationary states of an atomic system.

is polarised perpendicular to the field. This result may be simply interpreted on the basis of the general formal relation between the quantum theory of line spectra and the ordinary theory of radiation. In fact, it was shown in Part I that, for a conditionally periodic system possessing an axis of symmetry, we shall expect only two types of transitions to be possible. In transitions of the first type  $n_3$  remains unchanged, and the emitted radiation is polarised parallel to the axis of symmetry, while the transitions of the second type, in which  $n_3$  varies by one unit, give rise to a radiation of circular polarisation in a plane perpendicular to this axis (see page 34). In order to show that this agrees with the empirical rule of EPSTEIN, it may be noted in the first place that, for any component which might be ascribed to a certain transition in which  $n_3$  changes by a given entire number of units, there exists always another transition which will give rise to a radiation of the same frequency but in which  $n_3$  remains unchanged or changes by one unit, according to whether the given number is even or uneven. Next it will be seen that, in case of the effect of an electric field on the hydrogen spectrum, we cannot detect by means of direct observations the circular polarisation of the radiation corresponding to transitions of the second type; because, for each transition giving rise to a radiation of circular polarisation in one direction, there will exist another transition giving rise to a radiation which possesses the same frequency but is polarised in the opposite direction. Besides on the problem of the polarisations of the different components into which the hydrogen lines are split up in the presence of the electric field, the general considerations in Part I allow also to throw light on the question of the relative intensities of these components, by considering the harmonic vibrations into which the motion of the electron in the stationary states can be resolved. Compared with the problem of the relative intensities of the components of the fine structure of the hydrogen lines, the present problem is simpler in that respect, that the stationary states may be assumed to be a-priori equally probable. Since the different components, into which a given hydrogen line is split up in the electric field, correspond to transitions between pairs of states which for all components have very nearly the same values for the total energy, these states may therefore be expected to be of approximately equal occurrence in the luminous gas. According to the considerations in Part I, we shall consequently assume that for a given hydrogen line the relative intensities of the different STARK effect components, corresponding to transitions between different pairs of stationary states characterised by  $n_1 = n'_1$ ,  $n_2 = n'_2$ ,  $n_3 = n'_3$  and  $n_1 = n''_1$ ,  $n_2 = n''_2$ ,  $n_3 = n''_3$  respectively, will be intimately connected with the intensities of the radiations of frequency  $(n'_1 - n''_1) \omega_1 + (n'_2 - n''_2) \omega_2 + (n'_3 - n''_3) \omega_3$ , which on ordinary electrodynamics would be emitted by the atom in the two states involved in the transition in question;  $\omega_1$ ,  $\omega_2$  and  $\omega_3$  being the fundamental frequencies entering in the expression (31) for the displacement of the electron. In order to test how far such a connection is actually brought out by the observations, it is necessary to determine the numerical values of the amplitudes of the harmonic vibrations into which the

motion of the electron can be resolved. The examination of this problem has been undertaken by Mr. H. A. KRAMERS, who has deduced complete expressions for these amplitudes, by means of which it was found possible, for each of the hydrogen lines  $H_\alpha$ ,  $H_\beta$ ,  $H_\gamma$  and  $H_\delta$ , to account in a convincing way for the apparently capricious laws which govern the intensities of the components observed by STARK.<sup>1)</sup> This agreement offered at the same time a direct experimental support for the conclusions mentioned above: that there exist no stationary states corresponding to  $n_3 = 0$ , while the stationary states corresponding to other values of  $n_3$  are a-priori equally probable; and that transitions can only take place between pairs of stationary states for which  $n_3$  is the same or differs by one unit. A general discussion of these problems will be given by KRAMERS in the paper, mentioned on page 69 in the last section, in which also the problem of the intensity of the fine structure components is treated in detail.

In the former section and in the present we have seen, how the problems of the influence of the relativity modifications on the lines of the hydrogen spectrum and of the influence of an external electric field on this spectrum can be treated, by regarding the motion of the electron as a perturbed periodic motion, and by fixing the stationary states on the basis of the relation between the energy and the frequencies of the secular perturbations. As it was done originally by SOMMERFELD and EPSTEIN, both these problems can also be treated by means of the theory of the stationary states of conditionally periodic systems which allow of separation of variables in a fixed set of positional coordinates. If, however, we consider the problem of the simultaneous influence on the hydrogen spectrum of the relativity modifications and a homogeneous electric field of any given intensity, there does not exist a set of coordinates for which a separation of variables can be obtained. On the other hand it is possible, also in this case, to apply the general considerations about perturbed periodic systems developed in the preceding. In fact, with reference to the treatment given in § 3 of the problem of the fine structure of the hydrogen lines, it will be seen that the deviations of the orbit of the electron from a Keplerian ellipse in the problem under consideration

<sup>1)</sup> Note added during the proof. In recent papers H. NYQUIST (Phys. Rev. X, p. 226 (1917)) and J. STARK (Ann. d. Physik, LVI, p. 569 (1918)) have published measurements on the effect of an electric field on certain lines of the helium spectrum which is given by (35), if in (40) we put  $N = 2$ . As will be seen from (78), the differences between the frequencies of the components into which these lines are split up will, for the same intensity of the external electric field, be smaller than for the hydrogen lines. In conformity with this it was not possible, with the experimental arrangement used by the authors mentioned, to observe separately the numerous components to be expected on the theory, but only to obtain certain rough features of the resolution of the lines in question. For the interpretation of these observations a detailed consideration of the relative intensities to be expected for the different theoretical components is therefore essential; and, as it will be shown in KRAMERS' paper, it is possible, on the basis of the calculation of the amplitudes of the harmonic vibrations into which the motion of the electron in the stationary states can be resolved, to account satisfactorily for NYQUIST's and STARK's results.



will be the same as the secular perturbations produced on a Keplerian motion by the simultaneous influence of an external homogeneous field of force and an external central force proportional to the inverse cube of the distance from the nucleus. Since these two fields together form a perturbing field possessing axial symmetry, it follows therefore that the secular perturbations, when the relativity modifications are taken into account, will be conditionally periodic and that the problem of the stationary states may be treated by means of the method mentioned in § 2 on page 55. In this way we obtain in the first place the result, that, for any value of the intensity of the external electric field, we must expect that the hydrogen lines will be split up in a number of sharp components. Next, since for any value of this intensity different from zero the system will be non-degenerate, it follows from the conditions (61), that we must assume that the angular momentum round the axis of the field is always equal to an entire multiple of  $\hbar/2\pi$ ; in consistence with the assumption of the validity of the analogous condition involved in the fixation of the stationary states by means of the method of separation of variables, when applied to an explanation of the STARK effect with neglect of the relativity modifications (compare page 74). On the basis of the conditions (61) it is possible to predict in detail, how the fine structure of the hydrogen lines will be influenced by an increasing electric field until, for a sufficiently large intensity of this field, the phenomenon develops gradually into the ordinary STARK effect. The problem of this transmutation will be treated in a later paper by Mr. H. A. KRAMERS<sup>1)</sup>, who has kindly drawn my attention to this interesting application of the method of perturbations, and has thereby given a valuable impetus to the detailed elaboration of this method as regard the treatment of more complicate problems.

## § 5. The effect of a magnetic field on the hydrogen spectrum.

A theory of the ZEEMAN effect of the hydrogen lines based on the quantum theory of line spectra has, as mentioned in the introduction, been given independently by SOMMERFELD and by DEBYE. The calculations of these authors rest upon the fact, that it is possible, also in the presence of a magnetic field, to write the equations of motion of the electron in the canonical Hamiltonian form given by (4), if the momenta  $p_1, p_2, p_3$ , which are conjugated to the positional coordinates of the electron  $q_1, q_2, q_3$ , are defined in a suitable way. In complete analogy to the problem of the fixation of the stationary states of an atomic system when the relativity modifications are taken into account, it follows therefore that, if these equations

<sup>1)</sup> Besides the discussion of this problem, the paper in question will contain a general treatment of the theory of perturbed periodic systems from the point of view of the possibility of describing the motion by means of angle variables (compare Note on page 58).

can be solved by the method of separation of variables, we obtain, by fixing the stationary states by means of the conditions (22), a relation between the total energy of the atom in the presence of a magnetic field and the fundamental frequencies characterising the motion of the electron, which is exactly the same as that holding between the energy and frequencies in the stationary states of an ordinary conditionally periodic system. By a procedure analogous to that applied by BURGERS in his proof of the mechanical invariance of the relations (22) for slow changes of the external conditions, mentioned in Part I on page 21, it may further be proved that also in the presence of a magnetic field these relations are invariant, when regard is taken to the effect of the induced electric forces which, according to the ordinary theory of electrodynamics, will accompany a variation of the magnetic field. In the following, however, we shall not treat the problem of the influence of an external magnetic field on the hydrogen spectrum by means of the method of separation of variables, but in analogy to the treatment of the problems of the fine structure and of the STARK effect of the hydrogen lines, given in the preceding sections, we shall treat the problem from the point of view of the theory of perturbed periodic systems. Before entering on the detailed discussion of the necessary modifications to be introduced in the general considerations in § 2, in order that they may be applied also to the problem of the fixation of the stationary states of the atom in the presence of external magnetic forces, we shall for the sake of illustration first show how it is possible in certain cases to treat the problem of the effect of a homogeneous magnetic field on the hydrogen spectrum in a simple way, which will be seen to present a close formal analogy with the theory originally devised by LORENTZ on the basis of the classical theory of electrons.

In these considerations we shall make use of a well known theorem of LARMOR, which states that, if we look apart from small quantities proportional to the square of the intensity of the magnetic field, the motion of a system of electrons moving in a conservative field of force possessing axial symmetry round a fixed axis will, in the presence of an external homogeneous magnetic field parallel to this axis, differ from a mechanically possible motion of the system without field, only by a superposed uniform rotation of the entire system round the axis, the frequency of which is given by

$$\nu_H = \frac{e}{4\pi mc} H, \quad (79)$$

where  $H$  is the intensity of the magnetic field and  $c$  the velocity of light, while  $-e$  and  $m$  represent the charge and the mass of an electron.<sup>1)</sup> If the magnetic field

<sup>1)</sup> J. LARMOR, *Aether & Matter*, Cambridge 1900, p. 341. This theorem, which was established in connection with an attempt to develop a general theory of the ZEEMAN effect based on the ordinary theory of electrodynamics, is directly proved by observing that, with the degree of approximation in question, the accelerations of the electrons due to the presence of the magnetic field are equal to the changes in the accelerations of the particles due to the superposed rotation of the system.

is not constant, but if its intensity increases slowly and uniformly from zero, it is further simply shown that the electric induction forces, which will accompany the change in the intensity of the magnetic force, will just effect that a rotation as that described will be impressed on the original motion of the system.<sup>1)</sup> Moreover, as regards the effect of the magnetic field on the total energy of the system,<sup>2)</sup> it will be observed that the superposed rotation under consideration will not affect the mutual potential energy of the particles, while, with neglect of small quantities proportional to  $H^2$ , it will produce a change in the kinetic energy equal to  $2\pi P_0 H$ .

<sup>1)</sup> Compare P. LANGEVIN, *Ann. de Chim. et de Phys.* V, p. 70 (1905), who has deduced this result in connection with his well known theory of the magnetic properties of atomic systems based on the classical theory of electrons.

<sup>2)</sup> In an earlier paper (*Phil. Mag.* XXVII, p. 506 (1914)) the writer had assumed that the total energy in the stationary states of the hydrogen atom in the presence of a magnetic field would not be different from the energy in the corresponding states without field, as far as small quantities proportional to the intensity of the magnetic force are concerned; the effect on the kinetic energy of the electron due to the superposed rotation being assumed to be compensated by some kind of "potential" energy of the whole atom relative to the magnetic field. This assumption seemed not only suggested by the absence of paramagnetism in many elements, the atoms and molecules of which, according to the theory to be discussed in Part IV, must be expected to possess a resultant angular momentum, but it was especially thought to be supported by the fact, that the spectrum, emitted by hydrogen in the presence of a magnetic field, apparently did not form a combination spectrum of the type which should be expected, if the frequency of the radiation, emitted during a transition between two stationary states of the atom in the presence of the field, could be calculated directly from the values of the energy in these states by means of relation (1). As remarked by DEBYE (*Phys. Zeitschr.* XVII, p. 511 (1916)), this view, however, would not be reconcilable with EINSTEIN's theory of temperature radiation (see Part I, page 7) which implies the general validity of relation (1); and, moreover, as will be shown in the following, the ZEEMAN effect of the hydrogen lines may actually be considered, not as involving a deviation from the combination principle, but rather as affording an instructive example of a systematic disappearance of certain possible combination lines, for which a simple explanation can be obtained from a consideration based on the general formal relation between the quantum theory of line spectra and the ordinary theory of radiation. Further, with reference to this relation — and remembering that on ordinary electrodynamics the magnetic field will not directly influence the exchange of energy during a process of radiation, since the forces due to this field, being always perpendicular to the direction of the velocity, will not perform work on the moving electron — it seems also natural to assume that it is possible, simply from the effect of the superposed rotation on the kinetic energy of the electron, to determine the effect of the magnetic field, as regards the differences between the values of the energy in the different stationary states of the atom. Now, in a discussion of the spectrum to be expected on the quantum theory, we are concerned only with these differences and not with the absolute values of the additional energy of the system due to the presence of the magnetic field. It would therefore be possible to escape from the difficulty, mentioned above, as regards the absence of paramagnetism, by assuming that only the energy in the so-called "normal" state of an atomic system (i. e. the stationary state of the system which possesses the smallest value for the total energy; see Part IV) is not altered in the presence of a magnetic field, as far as small quantities proportional to the intensity of the magnetic force are concerned. On this view, the absence of paramagnetism would thus be a special property of the normal state, connected with the impossibility of spontaneous transitions from this state to other stationary states of the system. To this question we shall come back in the following parts of this paper; for the sake of simplicity, however, we shall not, in the considerations of this section, enter more closely on the consequences of the mentioned hypothesis, which would imply small modifications in the form of the following considerations, but would not affect the results.



where  $P$  represents the total angular momentum of the system round the axis, taken in the same direction as that of the superposed rotation.

From these results it follows that the motion of the electron in any stationary state of a hydrogen atom, which is exposed to a homogeneous magnetic field, will — if we look apart from small quantities proportional to the square of the intensity of the magnetic force and to the product of this intensity with the ratio between the mass of the electron and that of the nucleus — differ from the motion in some stationary state of the atom in the absence of the field, only by a superposed uniform rotation round an axis through the nucleus parallel to the magnetic force with a frequency given by (79). Due to the degenerate character of the system formed by the atom in the absence of the magnetic field, it is not possible, however, from a consideration of the mechanical effect produced on the motion of the electron by a slow and uniform establishment of the magnetic field, to fix the stationary states of the perturbed atom completely, but in order to fix these states we must consider more closely the relation between the additional energy of the system due to the presence of the magnetic field and the character of the secular perturbations produced by this field on the orbit of the electron. On the basis of LARMOR's theorem the discussion of this problem is very simple. In fact, since the frequency  $\nu_H$  is independent of the shape and position of the orbit, we may proceed in a manner which is completely analogous to that applied in the fixation of the stationary states of the hydrogen atom in the presence of a homogeneous electric field. Thus, looking apart from the effect of the relativity modifications, we may conclude at once that the total energy in the stationary states of the atom will be given by

$$E = E_n + n \nu_H h, \quad (80)$$

where  $n$  is an entire number which can be positive as well as negative, while  $E_n$  will be equal to the energy in the corresponding stationary state of the undisturbed atom, which is given by  $-W_n$  in (41). As in the case of the STARK effect, it will moreover be seen that this formula includes the values of the energy in such states of the atom, in which the electron moves in a circular orbit perpendicular to the direction of the field, and which beforehand must be expected to be included among the stationary states of the perturbed system, since such orbits during a slow and uniform establishment of the external field will not undergo secular perturbations as regards shape and position (compare page 73). In fact, since in these cases we have  $P = \pm n\hbar/2\pi$ , where  $n$  is the entire number characterising the stationary states of the undisturbed hydrogen atom, it follows from the above that the total energy in the special stationary states under consideration will just be represented by the formula (80), if we put  $n = \pm n$ . From this formula it will be seen at the same time, that the presence of the external magnetic field imposes the restriction on the motion in the stationary states of the hydrogen atom, that, with neglect of small quantities proportional to  $H$ , the angular momentum

of the electron round the axis of the field will be equal to an entire multiple of  $h/2\pi$ .

As regards the expression for the total energy of the hydrogen atom in the presence of the magnetic field, formula (80) is in agreement with the formulæ obtained by SOMMERFELD and DEBYE on the basis of the conditions (22), holding for conditionally periodic systems which allow of separation of variables. As shown by these authors, a system, which consists of an electron moving under the influence of the attraction from a fixed nucleus and of a homogeneous magnetic field, allows of separation of variables in polar coordinates, if the polar axis is chosen parallel to the magnetic field. Looking apart from the effect of the relativity modifications, and choosing for  $q_1$ ,  $q_2$  and  $q_3$  the length of the radius vector from the nucleus to the electron, the angle between this radius vector and the axis of the system, and the angle which the plane through the electron and this axis makes with a fixed plane through the axis respectively, they obtain the following expression for the total energy:<sup>1)</sup>

$$E = -\frac{2\pi^2 N^2 e^4 m}{h^2(n_1 + n_2 + n_3)^2} \pm \frac{ehn_3}{4\pi mc} H, \quad (81)$$

where  $n_1$ ,  $n_2$  and  $n_3$  are the integers which appear as factors to PLANCK's constant on the right side of the conditions (22). As mentioned this formula gives the same result as (80); in fact, if we put  $n = n_1 + n_2 + n_3$  and if we look apart from the small correction due to the finite mass of the nucleus, the first term in (81) is seen to coincide with the expression for  $-W_n$  given by (41), while the last term in (81) coincides with the last term in (80), if we put  $|u| = n_3$ . It will be observed, however, that, while in the theories of SOMMERFELD and DEBYE the stationary states are characterised by three conditions, only two conditions were necessary on the above considerations in order to secure the right relation between the energy and frequencies of the system in the stationary states. Thus, besides the conditions which prescribe the length of the major axis of the rotating orbit and the value of the angular momentum of the system round the axis of the field, the theories of the mentioned authors involve the further condition, that the value of the total angular momentum of the electron round the nucleus must be equal to an entire multiple of  $h/2\pi$ ; and that consequently the minor axis of the orbit has the same values as in a hydrogen atom perturbed by a small external central field (compare page 57). This is due to the circumstance, that the perturbed atom forms a degenerate system if we look apart from the effect of the relativity modifications, because the secular per-

<sup>1)</sup> A. SOMMERFELD, *Phys. Zeitschr.* XVII, p. 491 (1916) and P. DEBYE, *Phys. Zeitschr.* XVII, p. 507 (1916). While DEBYE proceeds directly by the application of the conditions (22) in a fixed set of positional polar coordinates, SOMMERFELD determines the stationary states by applying these conditions to the motion of the system relative to a set of coordinates which rotates uniformly round the polar axis with the frequency  $\omega_H$ ; a procedure which in the special case under consideration is simply shown to give the same result as the direct application of (22) to fixed polar coordinates.

turbations are simply periodic. From the point of view of separation of variables, this degenerate character of the system is in the present case, in contrast to the analogous case of the STARK effect, also directly revealed by the fact, that a separation can be obtained, not only in polar coordinates, but in any set of axial elliptical coordinates for which one focus is placed at the nucleus and the other at some point on the axis of the field. Just as in the case of the STARK effect, however, the system is no more degenerate as soon as the relativity modifications are taken into account, in which case a separation of variables will still be possible but only in polar coordinates. To this point we shall come back below.

The observations on the ZEEMAN effect of the hydrogen lines show that, if the fine structure is neglected, each line is in the presence of a magnetic field split up in a normal LORENTZ triplet; i. e. each line is resolved in three components of which the one is undisplaced and polarised parallel to the direction of the field, while the two other components possess frequencies, which differ from that of the original line by  $\nu_H$ , and are circularly polarised in opposite directions in a plane perpendicular to the direction of the field. As pointed out by SOMMERFELD and by DEBYE, the frequencies of a LORENTZ triplet are included among the frequencies of the components deduced from (81) by application of relation (1). In addition to the observed components, however, we might from (81) and (1) expect the appearance of a number of components, displaced from the original positions of the lines by higher multipla of  $\nu_H$ . For the non-appearance of these components the theories of SOMMERFELD and DEBYE offered no explanation, no more than for the polarisation of the components observed; except that SOMMERFELD in this connection draws attention to the fact, that the law governing the observed polarisations exhibits a certain analogy to the empirical rule of EPSTEIN concerning the observed polarisations of the components of the STARK effect of the hydrogen lines (see page 76). On the other hand, just as in case of the latter effect, an explanation of the number of the components observed and their characteristic polarisations is directly obtained on the basis of the general formal relation between the quantum theory of line spectra and the ordinary theory of radiation. In the first place we have at once from LARMOR's theorem, denoting the frequency of revolution of the electron in a stationary state of the undisturbed hydrogen atom by  $\omega$ , that the motion of the electron, in a corresponding stationary state of the atom in the presence of the field, may be resolved in a number of linear harmonic vibrations parallel to the direction of the magnetic force with frequencies  $\tau\omega$ , where  $\tau$  is a positive integer, and in a number of circular harmonic rotations perpendicular to this direction with frequencies  $\tau\omega + \nu_H$  or  $\tau\omega - \nu_H$ , according as the direction of rotation is the same as or the opposite of that of the superposed rotation. Next, with neglect of small quantities proportional to  $H^2$ , we have for the difference in the total energy between two neighbouring states of the perturbed system under consideration

$$\delta E = \delta E_0 + \delta \mathfrak{E} = \omega \delta I + \nu_H \delta \mathfrak{J}, \quad (82)$$



where  $E_0$  and  $\omega$  are the values of the energy and frequency and  $I$  is the value of the quantity defined by (5), all corresponding to the state of the undisturbed system which would appear if the magnetic force vanished at a slow and uniform rate, while  $\mathcal{E}$  is the additional energy due to the presence of the magnetic field and  $\mathfrak{J}$  the angular momentum of the system round the axis of the field multiplied by  $2\pi$  and taken in the same direction as that of the superposed rotation. Since (82) has exactly the same form as relation (66), and since in the stationary states we have  $I = nh$  and  $\mathfrak{J} = \mathfrak{n}h$ , we are therefore from a consideration, quite analogous to that given in § 2 on page 59, led to the conclusion, that, in the presence of the magnetic field, only two types of transitions between stationary states are possible. For both types of transitions the integer  $n$  may change by any number of units, but in transitions of the first type the integer  $\mathfrak{n}$  will remain constant and the emitted radiation will be polarised parallel to the direction of the field, while in transitions of the second type  $\mathfrak{n}$  will decrease or increase by one unit and the emitted radiation will be circularly polarised in a plane perpendicular to the field, the direction of the polarisation being the same as or the opposite of that of the superposed rotation respectively. Remembering that, with neglect of small quantities proportional to the magnetic force, the angular momentum of the system round the axis of the field remains unaltered in transitions of the first type and changes by  $h/2\pi$  in transitions of the second type, it will be seen that this conclusion is independently supported by a consideration of conservation of angular momentum during the transitions, like that given in Part I on page 34.

With reference to formula (80), it will be seen that the above results are in complete agreement with the experiments on the ZEEMAN effect of the hydrogen lines, as regards the frequencies and polarisations of the observed components. On the other hand, the observed intensities are directly accounted for, independent of any special theory about the origin of the lines. In fact, from a consideration of the necessary "stability" of spectral phenomena, it follows that the total radiation of the components, in which a spectral line, which originally is unpolarised, is split up in the presence of a small external field, cannot show characteristic polarisation with respect to any direction. In case of the ZEEMAN effect of the hydrogen lines, it is therefore necessary beforehand to expect that the intensity of the radiation, summed over all directions, corresponding to each of the three components in which every line is split up must be the same. From the point of view of the quantum theory of line spectra, it will be seen that by means of considerations of this kind we may inversely obtain a certain amount of direct quantitative information as regards the probabilities of spontaneous transition between different sets of stationary states, holding also in the region where the integers characterising these states are not large and where consequently the estimate of the values of these probabilities, based on the formal relation between the quantum theory and the ordinary theory of radiation, gives results which are only of an approximative character. This point will be discussed more closely in KRAMERS' paper on the relative

intensities of the components of the fine structure and the STARK effect of the hydrogen lines.

A procedure quite analogous to that applied above may be used to treat the problem of the effect of a homogeneous magnetic field on the hydrogen spectrum, also when the relativity modifications are taken into account, and when the atoms at the same time are exposed to a small external field of force of constant potential, which possesses axial symmetry round an axis through the nucleus parallel to the magnetic force: because also in this case we can obviously make direct use of LARMOR's theorem. We shall not, however, proceed in this way, but shall come back to these questions when we have shown how, by a simple modification of the general considerations of perturbed periodic systems given in § 2, it is possible to represent the theory of the stationary states of the hydrogen atom in the presence of a small magnetic field on a form, which allows to discuss the effect on the hydrogen spectrum also if the atom is exposed to a magnetic field which is not homogeneous, or to discuss the effect of a homogeneous magnetic field if electric forces, which do not possess axial symmetry round an axis through the nucleus parallel to the magnetic field, are acting on the atom at the same time.

In order to examine the general problem of the secular perturbations of the orbit of the electron in the hydrogen atom which take place if the atom is exposed to small external forces which, entirely or partly, are of magnetic origin, we shall, as in the usual theory of planetary perturbations, take our starting point in the equations of motion in their canonical form. Now the equations of motion of an electron of charge  $-e$ , which besides by an electric field of potential  $V$  is acted upon by a magnetic field of vector potential  $\mathfrak{A}$  (defined by  $\text{div } \mathfrak{A} = 0$  and  $\text{curl } \mathfrak{A} = \mathfrak{H}$ , where  $\mathfrak{H}$  is the magnetic force considered as a vector), can be written in the Hamiltonian form given by (4), if, just as in the absence of the magnetic field,  $E$  is taken equal to the sum of the kinetic energy  $T$  of the electron and its potential energy  $-eV$  relative to the electric field, while the momenta which are conjugated to the positional coordinates  $q_1, q_2, q_3$  of the electron in space are defined by the equations<sup>1)</sup>

$$p'_k = p_k - \frac{e}{c} \frac{\partial (\mathfrak{v} \mathfrak{A})}{\partial \dot{q}_k}, \quad (k = 1, 2, 3) \quad (83)$$

where the  $p$ 's are the momenta defined in the usual way (compare page 10), and where  $(\mathfrak{v} \mathfrak{A})$  represents the scalar product of the velocity of the electron  $\mathfrak{v}$  and the vector potential  $\mathfrak{A}$ , considered as a function of the  $q$ 's and of the generalised velocities  $\dot{q}_1, \dot{q}_2, \dot{q}_3$ . If we now assume that the effect of the magnetic forces on the motion of the electron is so small compared with the effect of the electric forces, that in the calculations we may look apart from all terms proportional to  $\mathfrak{H}^2$ , it is simply seen that the energy function  $E$  in (4), obtained by introducing the momenta defined by (83), will differ from the corresponding function, holding in

<sup>1)</sup> See f. inst. G. A. SCHOTT: Electromagnetic Radiation, App. F (Cambridge, 1912).

the absence of the magnetic field, only by the addition of a term which is linear in the momenta and equal to  $\frac{e}{c} (\mathfrak{V}\mathfrak{A})$ . In fact, denoting  $E$  expressed as a function of the  $q$ 's and  $p$ 's by  $\varphi(p, q)$ , we get from (83) together with (4), with the approximation under consideration,

$$E - \varphi(p', q) = - \sum_1^3 \frac{\partial \varphi}{\partial p'_k} (p'_k - p_k) = \sum_1^3 \frac{\partial E}{\partial p'_k} \frac{e}{c} \frac{\partial (\mathfrak{V}\mathfrak{A})}{\partial \dot{q}_k} = \frac{e}{c} \sum_1^3 \dot{q}_k \frac{\partial (\mathfrak{V}\mathfrak{A})}{\partial \dot{q}_k} = \frac{e}{c} (\mathfrak{V}\mathfrak{A}).$$

From this it follows that, with neglect of small quantities proportional to the square of the magnetic forces, the perturbations of the orbit of the electron in a hydrogen atom, which besides to a small external electric field of potential  $\phi$  is exposed to a small external magnetic field of vector potential  $\mathfrak{A}$ , are given by a set of equations of the same form as (44) in § 2, but where the  $\alpha$ 's and  $\beta$ 's are replaced by a set of quantities  $\alpha'_1, \alpha'_2, \alpha'_3, \beta'_1, \beta'_2, \beta'_3$ , which are related to the  $q$ 's and  $p$ 's and the time in the same way as the orbital constants  $\alpha_1, \alpha_2, \alpha_3, \beta_1, \beta_2, \beta_3$  for the undisturbed atom are related to the  $q$ 's and  $p$ 's and the time through the equations (18), and where  $\mathcal{Q}$  is replaced by the expression  $-e\phi + \frac{e}{c} (\mathfrak{V}\mathfrak{A})$ , considered as a function of the  $\alpha$ 's and  $\beta$ 's and the time. Since now, at any moment, the quantities  $\alpha'_1, \alpha'_2, \alpha'_3, \beta'_1, \beta'_2, \beta'_3$  differ from the corresponding orbital constants  $\alpha_1, \alpha_2, \alpha_3, \beta_1, \beta_2, \beta_3$  only by small terms proportional to the intensity of the magnetic field, we see therefore that, with neglect of small quantities of the same order as the variation in the orbital constants within a single period, the secular perturbations of the shape and position of the orbit of the electron will again be given by the equations (46), if in the present case  $\Psi$  is taken equal to the sum of the mean value  $\Psi_E$  of the potential energy  $-e\phi$  of the electron relative to the external electric forces and the mean value  $\Psi_M$  of the quantity  $\frac{e}{c} (\mathfrak{V}\mathfrak{A})$ , both taken over an osculating orbit corresponding to some moment during the revolution and expressed as functions of  $\alpha_1, \alpha_2, \alpha_3, \beta_2, \beta_3$ .<sup>1)</sup> The latter mean value, however, is easily seen to allow of a simple interpretation. In fact, we have

$$\Psi_M = \frac{e}{c} \frac{1}{\sigma} \int_0^\sigma (\mathfrak{V}\mathfrak{A}) dt = -\frac{e\omega}{c} B, \quad (84)$$

where  $\omega$  is the frequency of revolution of the electron in the osculating orbit, and where  $B$  represents the total flux of magnetic force through this orbit, taken in

<sup>1)</sup> If the relativity modifications are taken into account, the orbit of the electron in the undisturbed atom is not strictly periodic, but it will be seen that the secular variations of this orbit are still obtained from the equations (46), if only, to the expression for  $\Psi$  as defined in the text, a term is added which is equal to the expression for  $\Psi$  given by formula (70) in § 3.



the same direction as that of the magnetic force which would arise from the motion of the electron according to ordinary electrodynamics.

From the considerations in § 2 it follows now in the first place that, with neglect of small quantities proportional to the square of the external forces,  $\mathcal{V} = \mathcal{V}_E + \mathcal{V}_M$  will remain constant during the perturbations within a time interval, sufficiently long for the perturbing forces to produce a considerable change in the shape and position of the orbit of the electron; i. e. in a time interval of the same order as  $\sigma \lambda$ , if  $\lambda$ , just as in § 2, denotes a small quantity of the same order as the ratio between the external forces acting on the electron and the attraction from the nucleus. From a consideration analogous to that given in § 2, we may further conclude that, in the stationary states of the perturbed system, the quantity  $\mathcal{V} = \mathcal{V}_E + \mathcal{V}_M$  may be taken equal to the additional energy of the system due to the presence of the external fields. In fact, let us imagine that these fields are slowly established at a uniform rate within a time interval from  $t = 0$  to  $t = \vartheta$ , where  $\vartheta$  is a quantity of the same order as  $\sigma \lambda$ . For the total alteration in the inner energy of the system during this process we get then, with neglect of small quantities proportional to  $\lambda^2$ ,

$$\Delta_{\vartheta} a_1 = e \int_0^{\vartheta} \frac{t}{\vartheta} \sum_1^3 \frac{\partial \Phi}{\partial q_k} \dot{q}_k dt - \frac{e}{c} \int_0^{\vartheta} \frac{\omega B}{\vartheta} dt,$$

where the first term represents the work done on the system by the slowly increasing external electric forces, while the second term represents the work performed by the induced electric forces which accompany the variation in the intensity of the magnetic field. By partial integration of the first term, we get from this equation, with the approximation under consideration,

$$\Delta_{\vartheta} a_1 - e \Phi_{\vartheta} = -\frac{e}{\vartheta} \int_0^{\vartheta} \left( \Phi + \frac{\omega}{c} B \right) dt = \frac{1}{\vartheta} \int_0^{\vartheta} (\mathcal{V}_E + \mathcal{V}_M) dt = \frac{1}{\vartheta} \int_0^{\vartheta} \mathcal{V} dt. \quad (85)$$

Now the expression on the left side of this equation is equal to the change in the total energy of the system due to the establishment of the external field. Since the expression on the right side is seen to be a small quantity of the same order as  $\lambda a_1$ , it follows therefore from (85) in the first place that the secular variations of  $a_2, a_3, \beta_2, \beta_3$  during the increase of the fields will, just as in the case considered in § 2 (see page 47), be given by a set of equations of the same form as (46), where  $\mathcal{V}$  is replaced by  $\frac{t}{\vartheta} \mathcal{V}$ , and where again  $a_1$  may be considered as a constant. Also in the present case it follows therefore that  $\mathcal{V}$  will remain constant during the establishment of the external fields, and we see consequently that the expression on the right side of (85) will be simply equal to  $\mathcal{V}$ ; a result which, with reference to the principle of the mechanical transformability of the stationary states, leads to the

conclusion mentioned above, that the value of the additional energy in the stationary states of the perturbed system is given by the value of  $\mathcal{V}$  in these states.

From the above considerations it follows that the problem of the stationary states of the hydrogen atom in the presence of external electric and magnetic forces may be treated in a manner, which is exactly analogous to that applied in § 2 in case of a periodic system exposed to a small external field of constant potential. Thus, if the secular perturbations as determined by (46) are of conditionally periodic type, we shall expect that, with neglect of small quantities proportional to  $\lambda$ , the cycles of shapes and positions which the orbit of the electron passes through in the stationary states of the perturbed system will be characterised by the conditions (55), and that the possible values of the additional energy of the atom in the stationary states will be fixed by these conditions with neglect of small quantities proportional to  $\lambda^2$ . We shall therefore conclude that, also in the presence of external magnetic forces, the lines of the hydrogen spectrum will, if only the secular perturbations are of conditionally periodic type, be split up in a number of sharp components, the frequencies of which are determined by means of the conditions (67) together with relation (1). As regards the problem of the intensities and polarisation of these components, we may further proceed in a way quite analogous to that followed in § 2. In fact, if the secular perturbations are of conditionally periodic type, the displacement of the electron in any given direction may be represented as a sum of harmonic vibrations by an expression of the same type as (65). Moreover it can be proved that the difference in the total energy of two neighbouring states of the perturbed atom will again be given by the expression (66)<sup>1)</sup>. The general considerations in § 2 will therefore apply without alterations to the problem of the intensity and polarisation of the components into which the hydrogen lines are split up in the presence of small external forces, also if these forces are entirely or partly of magnetic origin. Similarly, it will be seen that the effect on the spectrum of a perturbed hydrogen atom, which will be due to the presence of a second external field small compared with the first, also in this case may be discussed directly by means of the considerations at the end of § 2.

We meet with a direct application of the preceding considerations, if the hydrogen atom is exposed to the simultaneous influence of an external electric and an external magnetic field, which possess axial symmetry round a common axis through the nucleus. Introducing the same set of orbital constants as described in § 2 on page 54, we get in this case that  $\psi_M$ , as well as  $\psi_E$ , and consequently the function  $\mathcal{V} = \mathcal{V}_E + \mathcal{V}_M$  which enters in the equations (46), will, besides on  $\alpha_1$ , depend on  $\alpha_2$ ,  $\beta_2$  and  $\alpha_3$  but not on  $\beta_3$ . The general character of the secular perturbations of the orbit of the electron will therefore be the same as in the case, considered in § 2, where the atom is exposed only to an

<sup>1)</sup> Compare Note on page 58. Also in the presence of small magnetic forces, it will be possible to describe the motion of the perturbed system by means of a suitably chosen set of angle variables, if only the secular perturbations are of conditionally periodic type.

electric field of axial symmetry, and the conditions which fix the stationary states of the perturbed atom will again be expressed by the relations (61). As regards the question of the probability of spontaneous transition between the stationary states, we get moreover, just as in § 2, from a consideration of the harmonic vibrations into which the motion of the electron can be resolved, that only two types of transitions will be possible; in transitions of the first type  $n_2$  remains unaltered, and the accompanying radiation is polarised parallel to the direction of the common axis of the perturbing fields; in transitions of the second type  $n_2$  decreases or increases by one unit, and the accompanying radiation will be circularly polarised in a plane perpendicular to this axis. In this connection it may be remarked, however, that the number of components, into which a given hydrogen line is split up in the presence of a magnetic field, will in general be double as large as the number of components which appear in the presence of an external electric field of axial symmetry. In fact, in the latter case the motions of the electron in two stationary states of the perturbed atom, corresponding to the same value of  $n$ , will be symmetrical with respect to a plane through the axis, and these states will possess the same values for the additional energy, if  $n_1$  is the same while the values of  $n_2$  are numerically equal but have opposite signs. On the other hand, if the atom is exposed also to a magnetic field, this will not hold, because the value of the function  $\psi_M$ , in contrast to the value of  $\psi_E$ , will not possess the same sign for two orbits which have the same shape and position relative to the axis, but for which the direction of revolution of the electron is reversed. Considering two states of the perturbed atom for which the values of  $n_1$  are the same and the values of  $n_2$  are numerically equal but have opposite signs, we get therefore, if the atom is exposed only to a magnetic field of axial symmetry, that the values of the additional energy will be equal with exception of the sign; while, if the atom is exposed to a magnetic as well as to an electric field, the additional energy in two such states will in general differ also as regards its numerical value. In contrast to what in general will take place if the atom is exposed to an electric field of axial symmetry, it will thus be seen that, if the hydrogen atom is exposed only to a magnetic field possessing axial symmetry, the ensemble of components into which a given hydrogen line is resolved will be completely symmetrical with respect to the position of the original line, as regards the frequencies as well as the intensities and polarisations. Moreover it follows from the above, that if we consider a hydrogen atom exposed to an electric field of axial symmetry and imagine that an external magnetic field, which possesses symmetry round the same axis, is gradually established, each component which appears in the presence of the first field only will split up into two components, in such a way that each component polarised parallel to the axis will split up into two components of the same polarisation, while each component polarised perpendicular to the axis, and which originally showed no polarisation when viewed in a direction parallel to the axis, will split up into two components showing circular polarisations in opposite directions. If the magnetic field is small, the new



components will be placed symmetrically with respect to the position of the original components and their intensities will be approximately equal, but when the perturbing influence of the magnetic forces on the motion of the electron becomes of the same order of magnitude as that of the external electric forces, the components in question will in general be placed unsymmetrically with respect to their original position, and their intensities may differ considerably.

An especially simple example of a magnetic field which possesses axial symmetry is afforded by the case of a homogeneous magnetic field, discussed in the beginning of this section. In this case we have that the total magnetic flux of force through the orbit of the electron is equal to the product of the intensity  $H$  of the magnetic field and the area of the projection of the orbit on a plane perpendicular to this field. Since this area is equal to  $a_3/2m\omega$ , we get consequently from (84)

$$\psi_M = \frac{e a_3}{2cm} H. \quad (86)$$

From the equations (46) it follows therefore that the effect of a homogeneous magnetic field, which acts upon a hydrogen atom which at the same time is exposed to an external electric field possessing axial symmetry round an axis through the nucleus parallel to the magnetic force, will consist in a superposition of a uniform rotation of the orbit round the axis with a frequency equal to

$$\nu_H = \frac{1}{2\pi} \frac{\partial \psi_M}{\partial a_3} = \frac{e}{4\pi mc} H$$

on the secular perturbations which would take place in the absence of the magnetic field. This result follows also directly from LARMOR's theorem, on which the simple considerations about the effect of a homogeneous magnetic field in the beginning of this section were based. Since a superposed rotation as that in question will not influence the shape of the orbit of the electron or its position relative to the axis, it follows from (61) that the value of  $\psi_E$  in the stationary states of the atom will not be affected by the presence of the magnetic field, and that consequently the effect of this field on the additional energy of the system will simply consist in the addition of a term given by

$$\psi_M = \frac{e}{2mc} \frac{n_2 h}{2\pi} H = n_2 \nu_H h. \quad (87)$$

This result was also to be expected from a simple consideration of the mechanical effect produced on the motion by a slow and uniform establishment of the magnetic field (compare page 81). With reference to the above considerations as regards the probability of transition between stationary states, it will be seen to follow from (87), that the presence of the homogeneous magnetic field will leave the components polarised parallel to the axis unaltered, but will cause every component, which in the absence of the field was polarised perpendicular to the axis, to split up in a

symmetrical doublet the members of which will show circular polarisation in opposite directions, when viewed in the direction of the axis, and will be displaced from the position of the original component by an amount corresponding to a frequency difference equal to  $\nu_H$ .

A simple application of the last result is afforded by the problem of the simultaneous effect on the hydrogen lines of a homogeneous electric and a homogeneous magnetic field which have the same direction. Thus, if the intensities of the fields are so large that we may look apart from the small modifications claimed by the theory of relativity, we shall from the above expect that the effect in question will differ from the ordinary STARK effect of the hydrogen lines, only therein that every component polarised perpendicular to the field is split up in two symmetrical components corresponding to the outer members of a LORENTZ triplet. This seems to agree with some observations of the effect of two such fields on the hydrogen line  $H_\alpha$ , published by GARBASSO.<sup>1)</sup> The problem in question might also have been treated by means of the method of separation of variables, because, as may be easily shown, the perturbed system — if the relativity modifications are neglected — allows of separation of variables in parabolic coordinates, just as in the presence of the electric field only. If, on the other hand, the relativity modifications are taken into account, the method of separation of variables cannot be applied, but, with reference to the considerations at the end of the last section, it will be seen that it is possible, also in this case, to predict at once the modification in the effect of an electric field on the fine structure of the hydrogen lines, which would result from the simultaneous presence of a parallel magnetic field. Passing to the limiting case where the intensity of the electric field is equal to zero, it will thus be seen at once from the preceding, that the effect of a homogeneous magnetic field on the fine structure of the hydrogen lines will consist in the splitting up of every component in a normal LORENTZ triplet. As far as the frequencies of the components are concerned, this result has been predicted by SOMMERFELD and DEBYE, who have treated the problem under consideration by means of separation of variables in polar coordinates (compare page 84). In connection with the fixation of the stationary states in this problem, it may be remarked that we must assume that no stationary state will exist for which the angular momentum round an axis through the nucleus parallel to the magnetic field would be equal to zero. In fact, as seen in § 4, we must assume that, in case of a hydrogen atom exposed to a homogeneous electric field, no such states will be possible; and by imagining that the electric field decreases slowly to zero, while at the same time a magnetic field parallel to the electric field is slowly established, it would be possible, without passing through a degenerate system, to obtain a continuous transformation of the stationary states of the perturbed atom during which the angular momentum of the electron round the axis would remain unaltered. With

<sup>1)</sup> A. GARBASSO, Phys. Zeitschr. XV, p. 123 (1914).

reference to the invariance of the a-priori probability of the stationary states during such a transformation (see Part I, page 9 and 27), we must therefore conclude that, also in the case of a hydrogen atom in the presence of a magnetic field, no stationary states exist for which the angular momentum round the axis would be equal to zero, although these states in mechanical respect do not exhibit singularities from which we might anticipate that they are physically unrealisable.<sup>1)</sup>

In case we consider the general problem of the effect on a hydrogen atom of a small electric or magnetic field, which do not possess axial symmetry round an axis through the nucleus, or of the simultaneous effect of two such fields, which do not possess such symmetry round a common axis, we must expect that the secular perturbations of the orbit of the electron will in general not be of conditionally periodic type. In such a case we cannot obtain a complete fixation of the stationary states, and we may conclude that the presence of the external forces will not give rise to the splitting up of the hydrogen lines into a number of sharp components but to a diffusion of these lines. With a simple example, in which the secular perturbations of the atom seem not to be of conditionally periodic type, we meet if we consider the simultaneous effect on the hydrogen spectrum of an external homogeneous electric field and a homogeneous magnetic field, the directions of which make an angle with each other. If

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<sup>1)</sup> Note added during the proof. In a dissertation which has just appeared, J. M. BURGERS (Het Atoommodel van Rutherford-Bohr, Haarlem 1918) has given a very interesting general survey of the applications of the quantum theory to the problem of the constitution of atoms, and has in this connection entered upon several of the questions discussed in the present paper; for instance on the question of the relation between the spectrum of an atomic system, deduced by application of relation (1) from the values of the energy in the stationary states, and the frequencies of the harmonic vibrations into which the motion in these states can be resolved; and on the question of the determination of the relative values for the a-priori probability of the different stationary states of an atomic system by means of EHRENFEST's principle of the invariance of these values during a continuous transformation of the system. As an illustration of the latter considerations, BURGERS has deduced an expression for the relative values of the a-priori probability of the different stationary states of the undisturbed hydrogen atom, by means of an enumeration of the states, determined by the conditions (22) when applied in connection with a separation of variables in polar coordinates, which correspond to a stationary state of the undisturbed atom, characterised by a given value of  $n$  in the condition  $I = nh$ . Excluding only such states for which the total angular momentum of the electron round the nucleus would be equal to zero, BURGERS (loc. cit. p. 259) finds in this way for the value of the a-priori probability in question  $(n+1)^2 - 1$ . In connection with the analogous consideration, given in the Note on page 76 of the present paper, which leads to a different result, it may be of interest to remark that the necessary conformity between the relative values for the a-priori probability of the different stationary states of the undisturbed hydrogen atom, deduced from an enumeration of the stationary states of the atom which appear in the presence of a small external electric field or in the presence of a small magnetic field respectively, cannot be obtained if in both cases we would exclude only such states in which the angular momentum of the electron round the nucleus is always equal to zero. In fact, while in case of a magnetic field this would give  $(n+1)^2 - 1$  different states corresponding to a given value of  $n$ , it would in case of an electric field give only  $(n+1)^2 - 2$  such states. On the other hand, if the possible stationary states are selected in the manner explained in the text, the conformity in question will obviously be obtained.



the effects of the two fields on the motion of the electron are of the same order of magnitude we may in this case expect that the hydrogen lines will not be resolved into sharp components but will become diffuse. From the considerations on page 60 of the effect on the spectrum of a perturbed periodic system due to a second external field, the perturbing effect of which is small compared with that of the first, we may conclude, however, that, if the effect of one of the fields on the motion of the electron is large compared with that of the other, the hydrogen lines will still show a resolution in a number of components, the spectral widths of which are small compared with the displacements which they have undergone due to the presence of the weaker of the external fields. In the discussion of this problem we shall for simplicity neglect the influence of the relativity modifications, assuming that the effect on the spectrum produced by each external field separately is large compared with the inherent fine structure of the hydrogen lines. Denoting, as in § 2, by  $\mu$  a small constant of the same order as the ratio between the forces on the electron due to the weaker of the external fields and those due to the stronger of these fields, and by  $\lambda$  a small constant of the same order as the ratio between the latter forces and the attraction from the nucleus, we have, as shown on page 61, that, with neglect of small quantities of the same order of magnitude as  $\lambda\mu^2$ ,<sup>1)</sup> the change in the additional energy of the atom due to the presence of the weaker field is, in general, directly obtained by taking the mean value of the function  $\Psi$ , corresponding to the weaker field, over the cycle of shapes and positions which the orbit of the electron passes through in the stationary states of the atom in the presence of the stronger field only. In the special case under consideration, however, the perturbed system, formed by the atom in the presence of the stronger field only, is degenerate, the secular perturbations of the orbit of the electron being of a simple periodic character. The mean value in question will therefore not be completely determined, but will be different for the different periodic cycles of shapes and positions of the orbit, which represent the continuous multitude of stationary motions which the electron may perform in each of the stationary states of the atom in the presence of the stronger field only. In order to fix the stationary states in the presence of both fields and the change in the additional energy of the atom due to the presence of the weaker field, it will thus, as mentioned on page 62, be necessary to examine the relation between the mean value in question and the frequency of the slow periodic "secular" variations which the cycles under consideration will undergo under the influence of the weaker of the external fields. Now, in the special case under consideration this problem may be treated very simply, if we imagine the weaker field as composed of two homogeneous fields of which the one is parallel and the other perpendicular to the stronger field, and if we consider separately the secular effect due to each of these fields. In fact, due to the symmetry

<sup>1)</sup> Rigorously this result holds with neglect of small quantities of the same order of magnitude as the largest of the quantities  $\lambda^2$  and  $\lambda\mu^2$ , but for the sake of simplicity it is here and in the following assumed that  $\mu$  is not smaller than  $\sqrt{\lambda}$  (compare page 61).

with respect to the axis of the stronger field, exhibited by the periodic cycle of shapes and positions which the orbit of the electron would pass through if the atom were exposed to this field only, it is easily seen that the contribution, which the perpendicular component of the weaker field gives to the mean value of  $\psi$  corresponding to the latter field, will vanish. From this it follows that the secular effect of the weaker field, with neglect of small quantities proportional to  $\mu^2$ , will be the same as if only the parallel component of this field was acting on the atom; and we see consequently that, in the stationary states of the atom in the presence of both fields, the possible cycles of shapes and positions of the orbit of the electron will be characterised in the same way as if the weaker field was parallel to the stronger. The problem, however, of the fixation of the stationary states of a hydrogen atom in the presence of a homogeneous electric field and a homogeneous magnetic field, which are parallel to each other, is very simple. In fact, as it appears from the considerations on page 91, the stationary states will in this case be fixed completely by two conditions, of which the one, in the same way as in the simple theory of the STARK effect, defines the position of the plane in which the electrical centre of the orbit of the electron moves, while the other defines the value of the angular momentum of the electron round the axis of the fields in the same way as in the simple theory of the ZEEMAN effect. In connection with the problem under consideration here, it may be useful for the sake of illustration to note, that, if the perturbing effect of the electric field is large compared with that of the magnetic, the second of these conditions may be said to be imposed on the system by the slow and uniform rotation, which the magnetic field produces on the periodic cycle of shapes and positions of the orbit of the electron, which would appear if the atom was exposed to the electric field only. If, on the other hand, the effect of the magnetic field is large compared with that of the electric field, the first condition may be said to be imposed on the system by the slow periodic oscillation in the shape and position relative to the axis, which the electric field produces on the uniformly rotating orbit which the electron would describe if the atom was exposed to the magnetic field only.

If we consider a hydrogen atom which is exposed to the simultaneous influence of a homogeneous electric field of intensity  $F$  and a homogeneous magnetic field of intensity  $H$ , the direction of which makes an angle  $\varphi$  with the direction of the electric field, it follows from the above that, if the perturbing influence of the electric field is large compared with that of the magnetic field, the main effect produced by the latter field on the spectrum may be described as the splitting up of each STARK effect component, polarised perpendicular to the axis of the electric field, into two circularly polarised components, corresponding to the outer members of a LORENTZ triplet which would be produced by a magnetic field of intensity  $H \cos \varphi$ . On the other hand, if the perturbing effect of the magnetic field is large compared with that of the electric, it follows that the main effect, produced by the latter field on the spectrum, may be described as the resolution of the middle component and

of each of the outer components of the normal ZEEMAN effect into a number of components, corresponding to the parallel and perpendicular components respectively of a STARK effect produced by an electric field of intensity  $F \cos \varphi$ .

The effects just described, however, which are the same as would take place if only the parallel component of the weaker field was acting on the atom, will not be the only effects of the presence of the weaker field on the spectrum. In fact, although the perpendicular component of the weaker field, apart from small quantities proportional to  $\mu^2$ , will not have any secular effect on the cycle of shapes and positions which the orbit of the electron would pass through if the atom was exposed to the stronger field only, it will obviously produce alterations in the motion of the electron within this cycle which are proportional to  $\mu$ . Thus, if the weaker field was parallel to the stronger, the motion of the electron in the perturbed atom would be composed of a number of linear harmonic vibrations parallel to the direction of the fields, the frequencies of which are of the type  $\tau\omega_P + t_1\nu_1$ , and of a number of circular harmonic rotations perpendicular to this direction, the frequencies of which are of the type  $\tau\omega_P + t_1\nu_1 + \nu_2$  (compare page 59). In the general case, however, where the weaker field is not parallel to the stronger, there will, in the expression for the displacement of the electron in any given direction, in addition appear a number of harmonic vibrations the amplitudes of which are proportional to  $\mu$  and the frequencies of which, as a closer consideration of the perturbations learns, are equal to the sum or difference of the frequency of one of the harmonic vibrations, in which the motion in this direction could be resolved if the external fields were parallel to each other, and one of the small frequencies of type  $t_1\nu_1 - \nu_2$ , which appear in the expression for the secular perturbations of the electron in this case. A part of these additional vibrations will again possess frequencies of the types  $\tau\omega_P + t_1\nu_1$  and  $\tau\omega_P + t_1\nu_1 - \nu_2$ , and will cause that the motion, instead of consisting of vibrations which are exactly linear and exactly circular as in the case where the external fields are parallel to each other, will be composed of elliptical harmonic vibrations which partly are nearly linear and parallel to the direction of the stronger field and partly nearly circular and perpendicular to this direction. On account of this we shall expect that, due to the presence of the perpendicular component of the weaker field, the different components mentioned above will not be sharply polarised. Further there will, in the motion of the perturbed atom, also appear a number of circular harmonic rotations perpendicular to the stronger field, the amplitudes of which are small quantities proportional to  $\mu$ , and the frequencies of which are of the type  $\tau\omega_P + t_1\nu_1 - 2\nu_2$ . From this we shall expect the appearance in the spectrum of a number of new weak components, corresponding to a type of transition between stationary states which would not be possible if the two external fields were parallel to each other. When considering more closely the frequencies of these new components, it must be remembered, however, that, as mentioned above, the present method of treating the problem of the perturbations assures us of the conditionally periodic cha-



racter of the motion of the electron within a time interval of the same order of magnitude as  $\sigma/\lambda$ , only if we look apart from small quantities of the same order as  $\mu^2$ ; and we must therefore be prepared to find that the frequencies of the vibrations of small amplitudes will not be defined with the same degree of approximation as the frequencies of the vibrations of large amplitudes. Thus, while the frequencies of the latter vibrations are defined with neglect of small quantities proportional to  $\lambda\mu^2$ , the frequencies of the small vibrations under consideration are obviously defined only with neglect of small quantities proportional to  $\lambda\mu$ . In intimate connection with the general want of definition of the energy in the stationary states for perturbed systems of the type in question, we must accordingly be prepared to find that, in contrast to the strong components, for which we may expect that by far the larger part of the intensity is contained within a spectral interval of a width proportional to  $\lambda\mu^2$ , the new components will be diffused over spectral intervals of a width proportional to  $\lambda\mu$ .<sup>1)</sup> Thus, in case the effect of the external electric field is large compared with that of the magnetic field, we might expect at first sight that, on each side of every of the STARK effect components polarised parallel to the electric force, there would appear a weak component which would be circularly polarised and be displaced from this component by an amount twice that of the displacement of the strong components into which the perpendicularly polarised STARK effect components are split up as a consequence of the small magnetic field. We must be prepared, however, to find that these weak components will be so diffuse, that they are not separated from the weak perpendicular component which has the same frequency as the strong parallel components on each side of which the weak components under consideration would lie, and which appears as a consequence of the above mentioned want of sharpness as regards the polarisation of the strong components. On the other hand, if the effect of the magnetic field is large compared with that of the electric field, any weak component of the type under consideration, which corresponds to transitions in which the

<sup>1)</sup> Compare Note on page 61. With reference to the general validity of relation (1), it will be seen that the assumption, that the weak components possess this degree of diffusion, implies the assumption, that the corresponding transitions (the probability of occurrence of which is very small compared with the probability of the transitions responsible for the strong components) will generally take place between two states of the perturbed atom, which do not both belong to the well defined ensemble of stationary states in which at any moment the great majority among a large number of atoms will be present. Thus, in case the effect of the external electric field is large compared with that of the magnetic field, we may expect that, in both states involved in the transitions in question, the positions of the plane in which the electrical centre moves will coincide with positions of this plane in states belonging to the ensemble just mentioned, while the angular momentum of the electron round the axis of the electric field will generally change by an amount which will not be equal to an entire multiple of  $\hbar/2\pi$ . On the other hand, if the effect of the magnetic field is the larger, the angular momentum of the electron round the axis of this field will, in the transitions in question, change by two times  $\hbar/2\pi$ , while we may expect that the plane in which the electrical centre moves will generally, in at least one of the states involved in these transitions, differ from the positions of this plane in the ensemble of stationary states referred to.

angular momentum of the electron round the axis of the magnetic field changes by two times  $\hbar/2\pi$ , will lie at a distance from the original hydrogen line, which is approximately twice as large as that of the outer components of the normal ZEEMAN effect, and will therefore be distinctly separated from the strong components into which each of the components of the normal ZEEMAN effect is split up in the presence of the small electric field. We must be prepared, however, to find that the weak components will not, as it might be expected at first sight, form two sets of distinctly separated lines, but that they will only appear as two diffuse lines of circular polarisation in opposite directions and of a spectral width proportional to  $\lambda\mu$ .<sup>1)</sup>

## § 6. The continuous hydrogen spectrum.

We shall conclude the considerations of this Part by a brief discussion of the characteristic continuous spectrum of hydrogen in the ultra violet region, which is intimately connected with the series spectrum given by (35). This spectrum consists of a radiation, the frequencies of which are continuously distributed over a spectral interval extending from the head of the Balmer series in the direction of higher frequencies.<sup>2)</sup> The existence of a continuous spectrum of this type is just what should be expected from a natural generalisation of the principles underlying the quantum theory of series spectra.<sup>3)</sup> Thus the spectrum under consideration may be directly explained by application of relation (1), if we assume that the complete spectrum, emitted by a system consisting of a nucleus and of an electron, originates not only from radiations, emitted during transitions between two states belonging to the multitude of stationary states in which the electron describes a closed orbit, characterised by the condition  $I = nh$ , but also from radiations emitted during

<sup>1)</sup> No experiments, which allow to test the preceding results in detail, seem to have been recorded, but it would appear that the above considerations afford an explanation of the general character of the remarkable deviations from a normal ZEEMAN effect, observed by F. PASCHEN and E. BACK (Ann. d. Phys. XXXIX, p. 897 (1912)) in experiments in which the hydrogen lines were excited by passing a powerful condensed discharge through a capillary tube placed at right angles with the direction of the magnetic field. Besides the characteristic want of sharpness of the polarisation of the middle component, exhibited by all the spectrograms published by PASCHEN and BACK, especially one of their photographs (Tafel VIII, Bild 4) seems to suggest the presence of a weak, perpendicularly polarised, diffuse line on each side of the original line and at a distance from it twice that of the outer components of the normal effect.

<sup>2)</sup> This spectrum has been observed as an emission spectrum in spectra of solar protuberances and planetary nebulae (See J. EVERSHED, Phil. Trans. Roy. Soc. 197 A, p. 399 (1901) and W. H. WRIGHT, Lick Observatory Bulletin, No. 291 (1917)) as well as in direct laboratory experiments on spectra excited by positive rays (See J. STARK, Ann. d. Phys. LII, p. 255 (1917)). Further it has been observed as an absorption spectrum in the spectra of several stars (see W. HUGGINS, An Atlas of Representative Stellar Spectra, p. 85 (1899) and J. HARTMANN, Phys. Zeitschr. XVIII p. 429 (1917)).

<sup>3)</sup> Compare N. BOHR, Phil. Mag. XXVI, p. 17 (1913); and also P. DEBYE, Phys. Zeitschr. XVIII, p. 428 (1917).

transitions between two states, one (or both) of which belong to the multitude of states in which the electron possesses sufficient energy to remove to infinite distance from the nucleus. While the electron in the states of the type first mentioned may be said to be "bound" by the nucleus to form an atom, it may in the states of the last mentioned type be described as "free". In order to account for the appearance of the continuous spectrum, it is necessary to assume that the motions in the latter states are not restricted by extra-mechanical conditions of the type holding for the former states, but that all motions, which are consistent with the application of ordinary mechanics, will represent physically possible states. This assumption would also seem to present itself naturally from the point of view on the principles of the quantum theory, taken in the present paper.<sup>1)</sup> Thus it will in the first place be observed that any attempt to discriminate between the different states of the type in question, by means of considerations of the mechanical stability of stationary states for slow transformations of the external conditions, would fail on account of the essentially non-periodic character of the motion, which is irreconcilable with the idea of invariance of extra-mechanical conditions for such transformations. Next, with reference to the formal analogy between the quantum theory and the ordinary theory of radiation, it will be seen that the fact, that the motion of a free electron in its hyperbolic orbit cannot be resolved in a sum of harmonic vibrations of discontinuously varying frequencies but can only be represented by a Fourier integral extended over a continuous range of frequencies, suggests beforehand that the free electron may pass, under emission or absorption of radiation, to any one among a continuous multitude of other states corresponding to a continuous multitude of values for the energy of the system. From the preceding considerations we may infer, by application of (1), that the complete spectrum emitted by the hydrogen atom will, besides the series spectrum and the continuous ultra-violet spectrum mentioned above, which corresponds to transitions from a state in which the electron is free to a stationary state characterised by  $n = 2$  in (41), contain a set of continuous spectra, corresponding to transitions from free states to other stationary states, and each extending in the direction of larger frequencies from one of the values of the frequency, given by (35) if we put  $n' = \infty$ . Moreover, we may expect the presence of a weak continuous spectrum, extending as a continuous background over the whole region of frequencies, which will correspond to transitions between two different states in both of which the electron is free. The relative intensities of these different continuous spectra, and the laws according to which the intensity is distributed within each of them, may be expected to vary to a large extent according to the different conditions under which the radiation is excited. Thus,

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<sup>1)</sup> A view contrary to this has been taken by EPSTEIN, who in a recent paper (Ann. d. Phys. L, p. 815 (1916)) has made an attempt to obtain an explanation of certain observations on the photo-electric effect of hydrogen occluded in metals, by applying conditions of the same type as (22) to states of the hydrogen atom in which the electron describes a hyperbolic orbit, and has tried in a similar way to develop a theory of the characteristic  $\beta$ -ray spectra of radioactive substances.



while the continuous spectrum of hydrogen, when observed as emission spectrum in stars, shows a abrupt beginning at the head of the Balmer series, the continuous spectrum, observed by STARK in his experiments referred to above, was not sharply limited but showed a pronounced maximum in the spectral region which corresponds to transitions between two states, in the first of which the velocity of the free electron relative to the nucleus, before the "collision" with the latter, was of the same order of magnitude as the velocity of the positive rays by means of which the spectrum was excited.

Besides the series spectrum and the connected continuous spectrum just considered, there exists, as well known, another hydrogen spectrum, the so-called many-line spectrum, which on account of its complex structure and its resemblance with the band spectra, emitted by other elements and combinations of elements, is generally ascribed to the hydrogen molecule and not to the atom. This assumption would also seem to present itself directly from the point of view of the quantum theory, according to which the simple structure of the series spectrum is directly connected with the simple periodic character of the motion of the particles in the atom, while a spectrum of a complexity of the order exhibited by the many-line spectrum must be assumed to originate from a system the motion of which does not show such simple periodicity properties. The problem of the constitution of the hydrogen molecule, to be expected on the quantum theory, and the possible motions of the particles of this system will be treated in Part IV. In this connection we shall also consider the problem of dispersion of light in hydrogen gas and the problem of the voltage necessary to produce the lines of the series spectrum of hydrogen by an electric discharge in this gas.

## Part III.<sup>1)</sup>

### On the spectra of elements of higher atomic number.

#### § 1. General structure of series spectra.

According to Rutherford's theory we shall assume that the atoms of the elements consist of a number of electrons moving round a central nucleus of large mass and

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<sup>1)</sup> As it will appear from the introduction to the first part of this paper, it was the original plan in a treatise consisting of four parts to discuss from a uniform point of view the applications of the quantum theory to problems of atomic constitution. Already at the appearance of Part I a manuscript of the whole treatise existed, which to a large extent was ready for printing. For various reasons, however, only two parts were published at that time; besides the first part which appeared in March 1918, a second part which appeared in December 1918. This delay of the later parts was due in the first place to the nature of the subject. In fact already before the appearance of the second part it was felt necessary to change and to extend the original manuscript materially on account of the development of the theory brought about by the elaboration of the general ideas presented in Part I. A corresponding revision of the later parts, which was felt unavoidable, was however never brought to a satisfactory conclusion. Especially, the problem of the stability of atoms containing several electrons came more and more in the foreground and gave rise to difficulties which brought the limitation of the direct applicability of the general ideas as formulated in the first parts to light. A preliminary account of the results of my work with this problem in the last years is given in a lecture delivered about a year ago in the Physical Society of Copenhagen and published in Danish in *Fysisk Tidsskrift* XIX, p. 153, 1921, and in German in *Zeitschrift für Physik*. IX, p. 1, 1922. Together with two other lectures, delivered on previous occasions, in which the state of the theory at earlier stages of its development has been exposed, the lecture has moreover appeared in German in *Sammlung Vieweg* (*Drei Aufsätze über Spektren und Atombau*) and in English in a volume edited by the Cambridge University Press (*Three essays on spectra and atomic constitution*).

Under these circumstances the original plan has been abandoned, and the writer intends in a new series of papers to give a detailed account of the ideas and results exposed in the lecture referred to. On the other hand I have been advised on the part of several physicists to bring the treatise commenced to an end by publishing also the manuscript of the later parts, as far as it was ready for printing at the time when the first part appeared. Following this advice I herewith bring out Part III in the form which it had in the spring of 1918, with no alteration except such changes in the enumeration of the formulæ and in the references to the previous parts, which were necessitated by the subsequent extension of the manuscript of Part II before its publication in December 1918.

As will appear from the appendix, added at the end of this paper, several of the problems discussed in it have in the meantime been subject to investigations by various authors. This issue of Part III is therefore not to be considered as a scientific publication in the usual sense, the main intention with the publication of the original manuscript being to give the reader of the preceding parts an insight into some characteristic applications which the writer had in mind when exposing the general considerations in Part I, and therewith to bring the treatise to a natural conclusion. At the same time, however, the appendix referred to will give the reader a brief survey of the development of the theory since the redaction of the manuscript of this treatise.

of a positive charge, equal to that of the hydrogen nucleus multiplied by the "atomic number" of the element under consideration, i. e. by the number of the element in the periodic table. In considering the stationary states of such systems we meet in general with problems of great complexity. From the analogy of the series spectra of the elements with the hydrogen spectrum, however, we are at once led to the conclusion that the ordinary spectra of these elements are due to transitions between stationary states in which one of the electrons moves at a distance from the nucleus large compared to the distance of the other electrons, and in which this electron is therefore exposed to a force which differs only little from the force on the electron in the hydrogen atom<sup>1)</sup>. In fact this suggests a simple interpretation of the experimental result that in the ordinary series spectra of the elements, the so-called "arc spectra", the function  $f_r(n)$  in formula (2) on page 3 can be written

$$f_r(n) = -\frac{K}{n^2} \varphi_r(n) \quad (88)$$

where the constant  $K$  with a high approximation is found to be the same as the corresponding constant occurring in the formula (35) for the hydrogen spectrum and where  $\varphi_r(n)$  is a function which tends to unity when  $n$  becomes larger. In this way we obtain moreover an interpretation of the fact that the frequencies of the lines of the so called "spark spectra", which appear when the atoms of the elements are subject to a condensed discharge, can be represented by a formula which differs from the general formula holding for arc spectra only in the fact that the constant  $K$  is replaced by a constant which is four times larger<sup>2)</sup>. This is just what should be expected if these spectra originated from atoms which have lost one electron and in which another electron is removed at a large distance from the nucleus and thus exposed to a force which differs only little from the force which would be exerted by a single nucleus of double charge as that in the helium atom<sup>3)</sup>. For these reasons we shall in the following denote the arc spectra as series spectra of the first order, spark spectra as series spectra of the second order, and in general spectra in which the constant  $K$  is replaced by a constant  $m^2$  times larger, and originating from transitions between stationary states in which the atom has lost  $m-1$  electrons, while an  $m^{\text{th}}$  electron is removed to a distance from the nucleus, large compared with that of other electrons, as spectra of the  $m^{\text{th}}$  order.

These simple considerations on the other hand give no explanation of the characteristic difference between the hydrogen spectrum and the series spectra of other elements, which consists in the fact that while in the hydrogen spectrum, when the fine structure is neglected, there occurs only one function  $f_r(n)$  of the type (88) corresponding to  $\varphi(n) = 1$ , there appear in the spectra of other elements several such functions. On the basis of the general theory discussed in the preceding sect-

<sup>1)</sup> See N. BOHR, Phil. Mag. XXVI, p. 11 (1913).

<sup>2)</sup> See A. FOWLER, Phil. Trans. Roy. Soc. A. 214, p. 225, 1914.

<sup>3)</sup> See also N. BOHR, Phil. Mag. XXX, p. 407 (1915).



ions, however, the reason for this must obviously be sought in the fact that in the other elements the motion of the outer electron will, due to action of the inner electrons, not be simply periodic so that for a connection with the ordinary theory of radiation the existence of several series of stationary states is required. Thus, as pointed out by SOMMERFELD<sup>1)</sup>, a clue to the interpretation of the spectra under consideration is offered by his fundamental theory considered in Part I on page 17 of the stationary states of a system consisting of a particle moving in a central field of force. While for a simply periodic system the stationary states are characterized by the value of one integral positive number they are for this system determined by two such numbers  $n_1$  and  $n_2$  of which  $n_1$  serves to fix the value of an integral of the type (15) corresponding to the radial motion and  $n_2$  fixes the value of the angular momentum of the particle round the centre. Comparing the effect of the inner electrons with that of a central field of force the potential of which may be represented by a series of descending powers of the distance from the nucleus and putting  $n_1 + n_2 = n$  and  $n_2 = \tau$ , SOMMERFELD found that it is possible to obtain expressions for the energy in the stationary states which for constant  $\tau$  show a remarkable general resemblance with the empirical formulæ of Rydberg and Ritz for  $f_\tau(n)$  and which offer a suggestive interpretation of the fact that the empirical values of  $\varphi_\tau(n)$ , looking apart from the eventual complex structure of the lines, can for the spectrum of an element generally be arranged in a simple scheme of the following form:

$$\begin{array}{ccccccc} \varphi_1(1), & \varphi_1(2), & \varphi_1(3), & \varphi_1(4), & \dots\dots\dots \\ & \varphi_2(2), & \varphi_2(3), & \varphi_2(4), & \dots\dots\dots \\ & & \varphi_3(3), & \varphi_3(4), & \dots\dots\dots \\ & & & \varphi_4(4), & \dots\dots\dots \end{array}$$

in which  $\varphi_\tau(n)$  approaches to unity for constant  $\tau$  and increasing  $n$  as well as for constant  $n$  and increasing  $\tau$ . It will be observed that from this point of view the structure of the series spectra of the other elements is analogous to the hydrogen spectrum if the fine structure of the hydrogen lines is taken into account, and that the difference consists only in the fact that in the latter case, due to the much smaller deviations of the orbit of the electron from a periodic orbit, the functions  $f_\tau(n)$  show differences which are much smaller than the corresponding differences for the other spectra.

The above general view as regards the origin of the series spectra of the elements is supported in an instructive manner by the considerations of the former section about the probabilities of transitions between the different stationary states of an atomic system. Thus the displacement of an electron moving in a central field of force will be given by a set of expressions of the same type as that given by (73) on page 68, and we shall therefore assume that for this system only such transitions are possible in which  $n_2$  varies by one unit, or what is the same, in which the angular momentum of the electron decreases or increases by  $\frac{h}{2\pi}$ . This corresponds to the fact

<sup>1)</sup> A. SOMMERFELD, Ber. Akad. München, 1915, p. 425; 1916, p. 131.

that the frequencies of the lines in all the usual series in the visible spectra of the elements may be represented by  $\nu = f_{\tau''}(n'') - f_{\tau'}(n')$  where  $\tau'$  and  $\tau''$  differ by one unit. Thus in case of the arc spectra of the alkali metals the so-called Principal series may be represented by  $\nu = f_1(1) - f_2(n)$  ( $n = 2, 3 \dots$ ), the Sharp Subordinate series by  $\nu = f_2(2) - f_1(n)$  ( $n = 2, 3 \dots$ ) the Diffuse Subordinate series by  $\nu = f_2(2) - f_3(n)$  ( $n = 3, 4 \dots$ ) and the Fundamental series (Bergmann series) by  $\nu = f_3(3) - f_4(n)$  ( $n = 4, 5 \dots$ ).

The same holds for the great number of lines observed by FOWLER in his detailed investigation of the magnesium spark spectrum<sup>1)</sup>. Looking apart from the doubling of the lines, the combinations denoted by Fowler by  $P, S, D, p, C$  and the series denoted by  $s, d, f, A, B$  may in our notation be represented by the following scheme:

$$\begin{array}{ll} P = f_1(1) - f_2(2) & s = f_2(3) - f_1(n) \quad (n = 4, 5 \dots 7) \\ S = f_2(2) - f_1(2) & d = f_2(3) - f_3(n) \quad (n = 4, 5 \dots 8) \\ D = f_2(2) - f_3(3) & f = f_3(3) - f_4(n) \quad (n = 4, 5 \dots 11) \\ p = f_1(2) - f_2(3) & A = f_3(4) - f_4(n) \quad (n = 6, 7 \dots 12) \\ C = f_3(3) - f_2(4) & B = f_4(4) - f_5(n) \quad (n = 6, 7 \dots 12) \end{array}$$

The connection between the different series represented in this scheme, which is seen to be in agreement with the above considerations, coincides with that given by Fowler on the basis of the combination principle with the exception only of the  $B$  series the frequencies of which, according to Fowler, in our notation should be given by the combinations  $f_4(4) - f_4(n)$ . This would if correct be in disagreement with the rule that  $\tau$  must change by one unit, and it is therefore interesting to note that according to Fowler's calculations the  $B$  series was the only series for which apparently the frequencies observed showed deviations from the values deduced from the combination principle which surpassed the experimental errors (loc. cit. p. 253). All disagreement, however, disappears completely on the above interpretation of this series by introducing a fifth series of stationary states which according to the general theory must be expected to exist and to have values for the total energy corresponding to a function  $\varphi_5(n)$  which differs still less from unity than  $\varphi_4(n)$ .

The considerations about the probabilities of transition seem not only to account for the appearance of the observed series but seem also to be in general agreement with the relative intensities of these series. Thus the fact, that the amplitudes of the harmonic circular rotations into which the motion of an electron moving in a central field may be resolved will in general be larger if the direction of rotation is the same as that of the revolution of the electron than if it is opposite, offers a simple interpretation of the observation that the series in which the angular momentum during the transitions decreases are in general more intense than the series for which the angular momentum increases, and may explain that certain series of the latter type the existence of which should be expected on the theory have hitherto not been recorded. For a detailed discussion of this question, however, it would be

<sup>1)</sup> A. FOWLER, loc. cit.

necessary to take into account, that for an electron moving in a central field the stationary states corresponding to same  $n$  but different  $l$  will not be a-priori equally probable (Compare Part I p. 27).

## § 2. Series spectra of individual elements.

By means of a comparison with the spectrum to be expected from a system consisting of an electron moving in a central field of force we may thus explain certain general features of the series spectra of elements of higher atomic number. We cannot expect, however, that it is possible in this way to account in detail for the spectra of the elements, as is indicated already by the complex structure (doublets, triplets, satellites etc.), shown by the lines of many spectra. In a detailed discussion of these spectra it seems necessary to take the mutual perturbing effect of the orbits of the inner electrons and of the outer electron into account. In general this constitutes a very intricate problem due to the fact that already when the outer electron is absent, the system of inner electrons will in general be unstable for small displacements, if the effect of such displacements is calculated by means of ordinary mechanics. In case of helium, however, where there are only two electrons in the neutral atom, this is different since the motion of the inner electron will be mechanically stable for any shape or position of its orbit, if the outer electron is removed to infinite distance from the nucleus. Just in this property of the helium atom an explanation may be sought for the fact that helium, besides its simple spark spectrum, mentioned in Part II § 1, possesses two complete series spectra of the first order, the so called orthohelium and parhelium spectrum, for which no mutual combination lines are observed. This, which is seen to be in striking contrast to what should be expected for the spectrum of a simple central system, must be ascribed to the existence of two different sets of stationary states of the neutral helium atom corresponding to two different types of motion of the inner electron. This problem will be discussed in a later paper based on a detailed study of the mutual perturbations of the orbits of the two electrons in the helium atom performed in collaboration with Mr. H. A. KRAMERS, and it will be shown that it seems possible on the assumption that both electrons move in the same plane to obtain an interpretation of both helium spectra by means of considerations of the same kind as those applied in the preceding Parts.

In case of lithium, where the neutral atom contains three electrons, only one series spectrum of the first order is observed. In this case we may assume, that when one of the electrons is removed the two other electrons will move in the same circular orbit round the nucleus each with angular momentum  $\frac{h}{2\pi}$ , as in the normal state of the helium atom<sup>1)</sup>. Looking apart from the mechanical instability

<sup>1)</sup> See N. BOHR, Phil. Mag. XXVI, p. 489, 491 (1913).



of this system, the assumption presents itself, that the effect of the inner electrons on the outer due to their great frequency of revolution in comparison with that of the latter, to a high degree of approximation at any moment will be the same as that of an electric charge  $-2e$  distributed uniformly over a circle of radius equal to that of the orbit of the inner electrons in the absence of the outer electron. If we further would assume that the outer electron moves in the same plane as the inner electrons, we meet therefore with a case which can be treated by means of the simple theory of central systems. These assumptions have been used by SOMMERFELD<sup>1)</sup> in an attempt to explain the lithium spectrum, but apart from the interesting general resemblance with the formula of RYDBERG and RITZ mentioned in the former section, no close agreement with the observations could be obtained for any choice of the value of the radius of the orbit of the inner electrons. Thus the calculation gives, that for any value of this radius  $\varphi_r(n)$  should be smaller than unity for all values of  $r$ , while the observed values of  $\varphi_r(n)$  are slightly larger than unity except for  $r=1$ . For the latter value of  $r$  the observed values for  $\varphi_r(n)$  differ very considerably from unity and would, for its explanation, on SOMMERFELD's calculation claim a value for the radius of the inner orbit which would be far greater than that corresponding to the assumption mentioned above about the angular momentum of the inner electrons. These difficulties might arise from the mechanical instability of the inner system which may lead to considerable perturbations on the orbits of the inner electrons, especially in the case of  $r=1$ , where the outer electron during its motion passes close to these orbits. A possible explanation might also as remarked by SOMMERFELD be found in the assumption, that the electron would not move in the same plane as the inner electrons. In that case a simple calculation shows, that the outer electron would have a considerable perturbing effect on the orbit of the inner electrons in continuously changing the plane of these orbits. For the fixation of the stationary states for motions of these types the principles discussed in the former parts, however, would apparently not suffice. In contrast to the case of helium, no lithium spectra of higher orders have been hitherto observed. This may be understood on the assumption, supported by observations on absorption in vapours of alkali metals, that in the normal state of the lithium atom one of the electrons moves in an orbit outside that of the two other electrons, and that therefore this electron is far more easily removed from the atom than the other electrons. Under the exposure to a sufficiently intense discharge, however, we shall expect to observe two separate series spectra of the second order and one of the third. The first two spectra will correspond to transitions between stationary states in which one electron is removed and in which a second electron moves at a distance from the nucleus large compared with that of the third. These spectra may therefore be expected to be closely analogous to the two helium series spectra of the first order. The lithium spectrum of the third order will originate from atoms containing only

<sup>1)</sup> A. SOMMERFELD, Ber. Akad. München, 1916, p. 160.

one electron; it will therefore be quite analogous to the hydrogen spectrum and will be given by the formula (35), if  $K$  is replaced by  $9K$ .

If next we proceed to beryllium which is the fourth element in the periodic table and the neutral atom of which will therefore possess four electrons, we may expect that in the normal state of the atom the two electrons move in orbits outside the two others. The beryllium spectrum has not been investigated in great detail, but from the observations on the spectrum of magnesium, which is the next element in the Be group of the periodic table, we shall expect that beryllium will possess a series spectrum of the first order of a new type, different from that of the first order spectra of helium and lithium. This spectrum may be assumed to originate from transitions between states in which one electron moves at distances from the nucleus large compared with the three inner electrons, of which the one again moves in an orbit outside the two others. The essential difference between the spectrum under consideration and the helium spectra of the first order may be explained by the fact, that the outermost of the inner electrons in the beryllium atom moves in a field which differs considerably from that of a single nucleus of double charge, and its orbit will therefore not undergo perturbations under the influence of the outer electron of the same order of magnitude as that of the inner electron in the helium atom. In a discharge of greater intensity beryllium may next be expected to show a spectrum of the second order of the same type as the lithium spectrum of the first order. This is supported in an interesting way by the close analogy of the structure of the magnesium spark spectrum mentioned above with that of the ordinary arc spectra of the alkali metals. When exposed to sufficiently intense discharge we may further expect that beryllium will show two separate series spectra of the third order and one of the fourth order. Of these the two former spectra will be analogous to the helium series spectrum of the first order, while the latter will be of the same type as the hydrogen spectrum. In this way we may proceed to elements of higher atomic numbers. For each new element we shall expect, that there will appear a first order series spectrum of a new type together with spectra of the same types as those of the preceding elements but of higher orders. In this connection it will be observed that the well known similarity, referred to above, between the spectra of low orders of the different elements in the same group of the periodic table may be ascribed to the similar arrangement of the outer electrons in the atoms of these elements, indicated by the general similarity of the physical and chemical properties. The increasing number of inner electrons in the atom with increasing atomic weight of the elements within each group, however, may not only be expected to produce the gradual change of the position of the lines of these spectra, especially through the effect on the outermost of the inner electrons, but it would also seem likely that the presence of the inner electrons in some more direct way may be responsible for the rapidly increasing separation of the components of the lines (doublets, triplets etc.) with increasing atomic weight.

Even if we cannot account in detail for the effect of the inner electrons on

the outer electron by a comparison with a simple system consisting of an electron moving in a fixed central field we may assume, however, that the above general considerations as regards the appearance of the different series and their intensities will remain valid. In fact we may assume that the motion of the outer electron, due to the central character of the atom, can be resolved into a number of harmonic vibrations in a similar way as the motion of an electron in a simple central field. Moreover it will be observed that the considerations in Part I on page 33 about the change of angular momentum during the transitions are quite independent of the number of moving particles if only the field in which they move possesses an axis of symmetry.

### § 3. Effect of electric fields on series spectra.

The general analogy of the spectra under consideration with the spectrum to be expected for a simple system consisting of an electron rotating in a central field of force is also brought out very instructively by the effect of electric fields on these spectra, which has recently been investigated by STARK<sup>1)</sup> in case of a great number of elements. In case of a simple central system we shall except that the effect of the fields consists partly in the appearance of new spectral lines of intensities increasing with the electric field, partly in the splitting up of the different lines in a number of components polarized parallel and perpendicular to the direction of the electric force, just as in the problem of the influence of an external electric field on the fine structure of the hydrogen lines, considered in Part II. For a given field these effects will be the smaller the more the orbit of the electron in the stationary states involved in the transitions deviates from a purely periodic orbit. Now for the spectra of the elements a measure for these deviations may be sought in the deviations from unity of the values of the function  $\varphi_r(n)$  defined by (88)<sup>2)</sup>. For most spectra the latter deviations are considerable for small values of  $r$  and  $n$ , and in agreement with this STARK found that for the greater number of elements the effect on their spectra was exceedingly small or undetectable for electric fields of the intensities applied by him. In case, however, of the elements of smallest atomic numbers, viz. helium and lithium, the deviations from unity of  $\varphi_r(n)$  are much smaller, the difference  $\varphi_r(n) - 1$  being of the same order as 0,001 already for  $r = 3$ , and just for these elements STARK has found considerable effects which are of a very interesting nature.

In the first place the appearance of a number of new separate lines outside the usual series was observed in the presence of the field. These lines correspond

<sup>1)</sup> See J. STARK, *Elektrische Spektralanalyse chemischer Atome*, Leipzig 1914.

<sup>2)</sup> See N. BOHR, *Phil. Mag.* XXVII, p. 517 (1913) and XXX, p. 409 (1915).



to the series  $\nu = f_2(2) - f_2(n)$  ( $n = 4, 5, \dots$ ) in the orthohelium<sup>1)</sup> and lithium<sup>2)</sup> spectrum. For the same field the new lithium lines were more intense than the new orthohelium lines in conformity with the fact that the values of the functions  $q_2(n)$  differ less from unity for the lithium spectrum than for the orthohelium spectrum. As it should be expected from the comparison with the effect of an electric field on a system of one electron rotating in a central field it was further observed, that the new lines showed a characteristic polarisation relative to the direction of the electric force and were displaced more and more for increasing intensity of the field. In conformity with the theory the displacements observed were proportional to the square of the electric force for small fields, while for larger fields it became gradually proportional to the first power of the force. As regards the parhelium spectrum  $q_2(n)$  differs still less from unity than in lithium and we should therefore in this spectrum expect the appearance of new lines of the above mentioned series of still larger intensities than in the other spectra under consideration. These lines are not recorded by STARK as separate lines, but due to the close coincidence in this case of the lines of the new series and those of the ordinary diffuse series, the former enter as components in the complicated effects described by Stark as the electric "resolution" of the lines of the diffuse series. This is shown very clearly by some measurements of the effect of electric fields on the helium spectrum published quite recently by H. NYQUIST<sup>3)</sup> who has used the method of Lo SURDO which allows one to obtain on the same photograph the effect on the lines of electric fields of continuously varying intensities. Besides components which are formed by continuous displacement from the original lines, NYQUIST's photographs show that the mentioned resolutions of the two diffuse helium series contain components the intensity of which vanishes for vanishing field and which for decreasing field tend to positions at definite distances apart from the original line. In case of the parhelium spectrum these positions correspond in the first place to the lines  $\nu = f_2(2) - f_2(n)$ , but besides these lines there appear distinctly in the lower members of the diffuse series of both helium spectra components the positions of which for decreasing field converge to the lines given by  $\nu = f_2(2) - f_4(n)$  ( $n = 4, 5$ ). As regards Stark's observations of the "resolutions" in the electric field of the higher members ( $n = 5, 6, \dots$ ) of the diffuse series of the lithium spectrum and both helium spectra, we shall expect that for very small fields there will appear, besides the new lines mentioned above, a number of other new lines corresponding to  $\nu = f_2(2) - f_\tau(n)$  where  $\tau > 4$ . While according to the considerations on page 35 the new lines for which  $\tau'' - \tau'$  is either 2 or 0 for small fields should show intensities proportional to the square of the electric force, we shall expect that the intensities of the latter new lines which correspond to larger values of  $\tau'' - \tau'$  will increase proportionally to higher powers of this force. Due to the exceedingly small deviations from unity of the values of  $q_i(n)$  for such values

<sup>1)</sup> J. KOCH, Ann. d. Phys. XLVIII, p. 98, (1915).

<sup>2)</sup> J. STARK, Ann. d. Phys. XLVIII, p. 210, (1915).

<sup>3)</sup> H. NYQUIST, Phys. Rev. X, p. 226, 1917.

of  $\tau$ , we may assume, however, that already for values of the electric force small compared with those applied by Stark, the orbits in the corresponding stationary states will be perturbed very nearly in the same way as an orbit of the electron in the hydrogen atom. This explains the fact that for the fields applied the relative intensities of the components remained approximately constant, while their displacements were found to increase nearly linearly with the electric force, as in the case of the components of the Stark effect of the hydrogen lines discussed in the preceding section.

While a general interpretation of the effects of electric fields on the spectra of the elements of higher atomic number as regards the appearance of new lines may be obtained from a comparison with the effect to be expected on a spectrum originating from an electron moving in a central field of force, the detailed discussion of the displacement and splitting up of the components for increasing field, however, claims a closer consideration of the perturbations of the orbits of the inner electrons during the perturbations of the orbit of the outer electron in the presence of the external field. This problem will be considered at a later occasion in connection with the calculations on the helium spectrum mentioned above.

#### § 4. Effect of magnetic fields on series spectra.

As regards the effect of an external magnetic field on the spectra of elements of higher atomic number it would at first sight seem natural to assume that, in the presence of a magnetic field, just as in the case of hydrogen, the motion of the atom in a stationary state would differ from the motion in a stationary state without the field only by a superposed uniform rotation of frequency  $\omega_H$ , given by (79), round an axis through the nucleus parallel to the magnetic force. By applying as in Part II § 5, the general considerations of Part II § 2 about the relation between the energy and frequencies of an atomic system we should further conclude that the additional energy of the system due to the presence of the field was again given by the formula (80), and proceeding as in the paragraph mentioned we should expect that the effect of the field on the spectrum would, also for the spectra under consideration, consist in the resolution of every line in a normal Zeeman triplet. As well known this is not in general agreement with the observations, Although in certain cases, for instance in helium and lithium where the spectra consist of single lines or very narrow doublets, the resolutions observed to a high approximation are the same as those in hydrogen, we meet with far more complex effects, when we proceed for instance to the spectra of the alkali metals of higher atomic numbers, where the lines consist of doublets of considerable width. In the presence of a magnetic field each member of these doublets is resolved in a large number of components the displacements of which are proportional to the magnetic force, but

different for the two members of the doublet. For larger fields when the displacements of the components of these resolutions become of the same order of magnitude as the original width of the doublet the resolutions undergo, as shown by PASCHEN and BACH<sup>1)</sup>, gradual alterations until for very large fields all components of both members flow together into a normal Zeeman triplet. These effects which clearly have intimate connection with the unknown mechanism responsible for the doubling of the lines can obviously not be explained on the basis of the general considerations mentioned above. It would appear likely, however, that the difficulties in explaining the values of the additional energy in the atom in the presence of a magnetic field necessary to account for the anomalous effects by means of (1) are connected with the fact mentioned on page 81 that in the normal state of the atom, as shown by the absence of paramagnetism, the behaviour of the inner electrons cannot be determined by the simple considerations referred to.

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<sup>1)</sup> F. PASCHEN und E. BACH, Ann. d. Phys. XXXIX, p. 897, (1912).



## Appendix to Part III.<sup>1)</sup>

Note to § 1. The problem treated in this paragraph offers a simple application of the point of view developed in Part I and denoted there as a formal connection, or analogy, between the quantum theory and the classical electromagnetic theory of radiation. In order to prevent the possible misunderstanding that it is here a question of a direct connection between the description of the phenomena according to the quantum theory and according to classical electro-dynamics, in later papers of the author (compare Essay II) the law in which this analogy appears is designated as the "correspondence principle". It is a question indeed of a purely quantum theory theorem, which joins itself directly to the formulation of the fundamental principles of the quantum theory, and which affirms the existence of a connection between the possibility of any transition between two stationary states accompanied by radiation, and the appearance in the motion of a certain harmonic oscillation component which may be denoted as the oscillation "corresponding" to the transition. The application of the correspondence principle to the theory of series spectra given in this section has been already indicated in its outlines in Part I pages 46—50, and especially used in Part II, pages 97—99 in the discussion of the analogous problem of the fine structure of the hydrogen lines.

A treatment of the laws of series spectra from a formally similar point of view has been given meanwhile in a paper of SOMMERFELD and KOSSEL<sup>2)</sup>, and the question is treated in detail in Chapter VI of Sommerfeld's book "On Atomic structure and spectral lines"<sup>3)</sup>. As mentioned in this book, ROSCHDESTWENSKY had already called attention to the small modification demanded by the quantum theory in the combination scheme of the spark spectrum of magnesium given by FOWLER and referred to on page 104 of the text. This author has in the last years discussed in a series of papers<sup>4)</sup> the quantum theory classification of the experimental material of series spectra and has come to the conclusion, by a study of the empirical laws, that the fixation of the main quantum number  $n$  in the sharp series terms (S-terms) of the alkali metals is to be changed in such a way that in the first

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<sup>1)</sup> Compare the introductory note to Part III, p. 101. In the following the three lectures mentioned in this note will for brevity be referred to as Essay I, II and III respectively.

<sup>2)</sup> W. KOSSEL and A. SOMMERFELD, *Verh. d. Deutschen Phys. Ges.* 21, p. 240 (1919).

<sup>3)</sup> A. SOMMERFELD, *Atombau und Spektrallinien*, Vieweg. 3d ed., 1922. An english translation of this book has just appeared.

<sup>4)</sup> D. S. ROSCHDESTWENSKY. Transactions of the optical institute in Petrograd (Berlin).

S-term  $n = 2$  is to be put instead of  $n = 1$ . SCHRÖDINGER has come to the same conclusion by means of the assumption that, in the stationary states corresponding to the S-terms of the sodium spectrum, we have to do with a motion of the series electron in which during each revolution the electron gets into the region of the inner electron orbits<sup>1)</sup>, and that therefore the quantum number  $n$  in none of these states can be less than 2. The significance of this fact was at the same time pointed out by the writer<sup>2)</sup> in connection with the general considerations on the structure and stability of atoms mentioned in the note to § 2. As has been pointed out in Essay III, these considerations lead to the assumption that an essential change in the quantum numbers entering into the classification of the spectral terms is to be introduced. While it will be clear from the application of the correspondence principle given in the text, that the values of the quantum number designated by  $\tau$  are to be kept unaltered, it is shown that for instance in the spectra of the alkali metals the values for the main quantum number  $n$ , given in the diagram on page 103 can only be maintained for the series of terms corresponding to  $\tau$  equal to or larger than 3. The first S-term in these spectra will correspond to an orbit of the series electron, whose main quantum number increases by one unit, if we advance in the periodic system to the next group of elements. Thus for this orbit we have in lithium  $n = 2$ , in sodium  $n = 3$  etc. A corresponding change is also to be introduced in the main quantum numbers corresponding to the P-terms in these spectra. While, as in the diagram on page 103, in lithium the first P-term is to be characterized by  $n = 2$ , this term in sodium corresponds to  $n = 3$ , in potassium to  $n = 4$  etc.

Note to § 2. The considerations given in this paragraph can not in the details be maintained in the present state of atomic investigation. In fact, several of these considerations are especially fitted to emphasize the chief difficulties mentioned in the introductory note to Part III (p. 101). This refers particularly to the remarks concerning the stability of electronic orbits in atoms. However, we shall find that certain general statements concerning the change of series spectra of different order with increasing atomic number are essentially adequate. Thus it will be seen, that the remarks touching on this point are, in content, equivalent to the laws designated as the "spectroscopic displacement theorem" by SOMMERFELD and KOSSEL in their above mentioned paper, which have proved themselves very fruitful for the classification of the spectra as is shown in SOMMERFELD's book. Already concerning this point the later investigations on atomic structure, however, have led to the conclusion, that deviations from the laws in question are to be expected in the later periods of the periodic system, in that here with increasing atomic number we have to do not always with a repetition of the configuration of the inner electron system with an equal number of electrons, but, as pointed out in Essay III, we meet in

<sup>1)</sup> E SCHRÖDINGER, Zeitschr. für Phys. 4, p. 347 (1921).

<sup>2)</sup> Cf. "Nature", Vol. 107, p. 104 and Vol. 108, p. 208 (1921).

certain cases a transitory stage of development of the inner groups of electrons. Such gradual developments are responsible for the appearance of families of elements like the iron metals and the rare earths. Characteristic examples of the effect of a development of this kind on the structure of spectra are revealed in a recent important paper of CATALÁN on the series spectra of manganese<sup>1)</sup>.

As far as the discussion of the individual spectra is concerned, already in the case of helium the statements must be changed in essential points. Even if we must, indeed, maintain that the peculiar properties of the first order helium spectrum rest in the fact, that the orbit of the inner electron, on account of its approximately simply periodic character, is influenced in a much more thoroughgoing way by the forces originating from the outer electron than is the case in the inner system for other series spectra, the interpretation of the origin of the parhelium spectrum as well as of the normal state of the atom indicated here, is to be fundamentally changed. Concerning the first point LANDÉ<sup>2)</sup> has in two papers investigated the helium spectrum, coming to the conclusion that only to orthohelium are to be ascribed stationary states in which the two electrons move in one and the same plane; that, however, in the case of parhelium the orbital planes make an angle with each other. Although the discussion of the perturbations given by LANDÉ is open to serious objections, yet the continuation of the work by Dr. KRAMERS and the writer has led to conclusions which are in general agreement with these chief results. Concerning our detailed calculations, the publication of which has hitherto been put off due to various circumstances, we hope to report in the near future.

Concerning the normal state of the helium atom, the important experimental researches of FRANCK and his co-workers<sup>3)</sup>, published in the meantime, have shown conclusively that this state can not be a simple ring configuration as assumed in the text and does not at all belong to the coplanar orthohelium states, but must be regarded as the final state of the binding process corresponding to the emission of the parhelium spectrum. It appears possible to throw light on this point, by means of the correspondence principle, in a way which seems to offer a clue to the understanding of the stability of atomic structure in general. This is thoroughly reported on in Essay III where it is shown that for the discussion of this stability ideas based on ordinary mechanics do not suffice, and that we are led to a view on atomic structure which presents a type of symmetry of the electronic motions essentially different from that of the simple ring configurations previously adopted. From the considerations given there it will also be inferred, that the interpretations given in the text of the lithium spectrum and the spectra of other elements are to be changed essentially.

Finally concerning the question, touched on at the end of the paragraph, of

<sup>1)</sup> CATALÁN, Trans. Roy. Soc. A 223, p. 127 (1922).

<sup>2)</sup> A. LANDÉ, Phys. Zeitschr. 20, p. 228 (1919) and 21, p. 114 (1920).

<sup>3)</sup> J. FRANCK and F. REICHE, Zeitschr. für Phys. 1, p. 154 (1920), J. FRANCK and P. KNIPPING, Zeitschr. für Phys. 1, p. 320 (1920).



the origin of the complex structure of the series lines it has become clear through investigations in recent years, especially by SOMMERFELD<sup>1)</sup> and LANDÉ<sup>2)</sup>, that here we have to do with the appearance of a third quantum condition in the fixation of the orbit of the outer electron. This arises simply from the deviation from central symmetry of the field, in which the series electron moves and corresponds to the fixation of the stationary states of a hydrogen atom in an external field with axial symmetry (cf. Part II, page 54), of which we meet a characteristic example in the case of a hydrogen atom in a homogeneous external electric or magnetic field, when the relativity modifications of the equations of motion are taken into account (cf. Part II page 78 and 92). By the introduction of the third quantum condition the orbital plane of the series electron is fixed relative to the axis of the inner system, in such a way that the total angular momentum of the atom is equal to  $\mu \frac{h}{2\pi}$ , where  $\mu$  is a whole number, the third quantum number, which, together with the quantum numbers  $n$  and  $\tau$ , completely determines the state of motion of the series electron. Through this circumstance it is possible to a certain extent to restrict the transition possibilities by making use of considerations on the conservation of angular moments during the radiation process of the kind set forth in Part I, page 34, and independently developed by RUBINOWICZ (compare Part II, note on page 60). Thus we can conclude that in a transition the total angular momentum of the atom must remain constant or increase or decrease by  $\frac{h}{2\pi}$ . This restriction in the possibilities of variation of the quantum number  $\mu$ , which is in agreement with the observations, follows also directly from the correspondence principle, as is easily shown by a simple consideration, quite similar to the considerations in Part I, page 33 and Part II, page 59. It may, however, be pointed out, that the restriction in the variation possibility of the quantum number  $\tau$ , which is responsible for the remarkable limitation in the applicability of the general principle of combination of spectral lines, appearing in the characteristic structure of the series spectra discussed in § 1, can not be derived from considerations of the conservation of angular momentum, but is to be looked upon as a characteristic consequence of the correspondence principle. In contradiction to what has often been assumed (cf. Essay II, page 58; see also Sommerfeld's book, Ch. 6, § 2) and to what also has been indicated in the conclusion of the paragraph to which the present note refers, considerations of conservation of angular momentum can be used only to throw light on such limitations in the combination principle of spectral lines, which show themselves in the laws holding for the number of components of the complex structure of the individual series lines.

Note to § 3. The conclusions in this section rest upon the general considerations of disturbed systems developed in Part I, pages 49-50, and Part II, § 2, and

<sup>1)</sup> A. SOMMERFELD, *Ann. d. Phys.* 63, p. 221 (1920).

<sup>2)</sup> A. LANDÉ, *Zeitschr. f. Phys.* 5, p. 231 (1921).

represent in all essential points the present status of the theory. The experimental material on the Stark effect of the series spectra has been largely increased since the writing of the manuscript; first by the detailed investigations of STARK and LIEBERT on the appearance of new lines in the helium and lithium spectra, which have already been mentioned in Part II (cf. footnote on page 78), and which fulfill in all details the theoretical expectations described in the text. Further valuable material has been produced by the investigations of TAKAMINE<sup>1)</sup> on various spectra as well as by a thorough-going investigation of the Stark effect of the mercury spectrum, which this investigator has carried out in Copenhagen in collaboration with HANSEN and WERNER, and the results of which have revealed a variety of important details<sup>2)</sup>. The effects found in all these investigations are in close agreement with the theoretical anticipations, in that the main effect is the appearance of new polarized components, the intensities and displacements of which are closely connected with the relation of the spectral terms in question to the corresponding hydrogen terms.

Concerning the closer development of the theory subsequent to the writing of the manuscript the analogous problem of the influence of external electric forces on the fine structure of the hydrogen lines has been treated in detail by KRAMERS. His results, which are based on a complete mathematical treatment of the mechanical properties of the perturbed hydrogen atom, were already at hand at the final redaction of the second part of this treatise as will be seen from the discussion in Part II § 3, and have been meanwhile published in two papers<sup>3)</sup>. In the first of these papers it is shown, how we can arrive at a quantitative evaluation for the intensities with which in an electric field the additional fine structure components appear, which correspond to the new lines excited by the field in the series spectra of other elements, and the displacements of the individual fine structure components, initially proportional to the square of the field intensity, are calculated. In the second paper a complete discussion is given of the behaviour of the fine structure components for increasing electric field and of their gradual change into the ordinary Stark effect, where the displacement of the components has become directly proportional to the field intensity. By the same procedure it is possible to account for the effect of an external electric field on a hydrogen atom disturbed by an arbitrary central field, and thereby essentially to develop the considerations given in the text in their quantitative aspect. A calculation of this kind, concerning the initial displacement of the components, has been recently used by BECKER<sup>4)</sup> in order to discuss the Stark effect of the alkali spectra. Although an agreement in the order of magnitude

<sup>1)</sup> T. TAKAMINE, *Memoirs of the College of Science, Kyoto Imperial University, and Astrophys. Journ.* 50, p. 23 (1919).

<sup>2)</sup> H. M. HANSEN, T. TAKAMINE and S. WERNER: *D. Kgl. Danske Vid. Selsk. Skrifter* (under press).

<sup>3)</sup> H. A. KRAMERS, *Intensities of spectral lines*, *D. Kgl. Danske Vid. Selsk. Skrifter*, 8, Række III. 3 (1919), and *Zeitschr. für Phys.* 3, p. 199 (1920).

<sup>4)</sup> R. BECKER, *Zeitschr. für Phys.* 9, p. 332, 1922.

was attained, nevertheless these calculations are open to the objection, mentioned by BECKER himself, that they rest on assumptions concerning the character of the orbit of the outer electron in the stationary states, which in many cases are not in agreement with the above mentioned recent view on atomic structure, in consequence of which the main quantum numbers of the sharp series terms and of the principal series terms for sodium and the following alkali metals are to be changed (comp. page 113) Wholly aside from difficulties of this kind, a complete theoretical treatment of the effect of an electric field on the series spectra cannot be given, however, on the basis of such a calculation, because the deviations from a simple central field exhibited by the forces originating from the inner system, which are responsible for the complex structure of the individual series lines, will as already pointed out in the text, influence essentially the action of the external field. A detailed theoretical treatment of this influence, which shows itself especially clear in the abovementioned new investigations on the mercury spectrum, is, however, not yet at hand.

Note to § 4. The considerations given in the text on the anomalous Zeeman effect are of a very summary character, this subject at the time of the redaction of the manuscript being still very little developed. In the meantime an essential advance in the explanation of the experimental material in the sense of the quantum theory has been made by the systematic investigations of LANDÉ<sup>1)</sup> on the spectral terms by combination of which the frequencies of the components of the anomalous Zeeman effect may be represented. Also the promising discussion given by SOMMERFELD<sup>2)</sup> concerning the variations of these terms with increasing field, corresponding to the Paschen-Back effect must be mentioned here. The closer significance of the stationary states to be associated with the combination terms appears, however, still to offer fundamental difficulties and the interesting attempt, which HEISENBERG<sup>3)</sup> has made to get around these, does hardly possess sufficient connection with the principles which underlie the other applications of the quantum theory to atomic structure. As pointed out in the text the difficulty consists in the first place in the fact, that the ordinary electro-dynamic laws can no longer be applied to the motion of the atom in a magnetic field in the same way as seemed to be the case in the theory of the hydrogen spectrum<sup>4)</sup>. The conclusion mentioned in the text, that on the basis of the

<sup>1)</sup> A. LANDÉ, Zeitschr. für Phys. 5, p. 231 (1921).

<sup>2)</sup> A. SOMMERFELD, Zeitschr. für Phys. 8, p. 257 (1921).

<sup>3)</sup> W. HEISENBERG, Zeitschr. für Phys. 8, p. 273 (1921).

<sup>4)</sup> The theoretical expectation discussed in Part II, p. 72, that in a magnetic field each of the components of the fine structure of the hydrogen lines (and helium spark lines) will split up in a normal triplet, is strongly supported by an investigation of HANSEN and JACOBSEN (D. Kgl. Danske Vidensk. Selsk. math.-fys. Meddelelser III, 11, 1921) on the effect of a magnetic field on the helium spark line 4686 Å. Although this investigation was very difficult due to the sensitiveness of the fine structure of this line for electric forces present in the discharge, the result would at any rate seem to prove that the effect of the field is of a type entirely different from the anomalous Zeeman effect on other spectra. Compare also O. OLDENBERG, Ann. d. Phys. 67, p. 253 (1922).



correspondence principle we can directly conclude that the Larmor theorem in general does not hold for atoms containing several electrons, obtains further confirmation from the observations of PASCHEN and BACK<sup>1)</sup>, according to which in the magnetic field new components arise in the complex structure of the series lines, which correspond to transitions where the third quantum number changes by more than one unit. In fact from this phenomenon we may conclude that the magnetic field exercises a direct influence on the motion of the series electron relative to the inner system.

As mentioned in the text, these circumstances seem to be connected with the general character of the magnetic properties of the atoms of the elements in their normal state. Although this problem is still unsolved, a clue to the interpretation of these properties seems, as pointed out in Essay III, to be afforded by the circumstance, that the occurrence of atomic paramagnetism is most intimately connected with the presence in the atom of inner groups of electrons, which are in a state of further development and which therefore display a marked lack of symmetry.

<sup>1)</sup> F. PASCHEN and E. BACK, *Physica*, 1, (Zeeman jubilee number) S. 261 (1921).

At the conclusion of this work I wish to thank my collaborators for their valuable help, especially Dr. H. A. KRAMERS, who has not only contributed materially to the subject, but has also kindly assisted me in the redaction of the manuscript of all three parts of this treatise. On this occasion I wish also to express my sincere thanks to the direction of the Carlsbergfond for considerable grants in a number of years, which have enabled me to acquire assistance in the elaborate calculations on special problems underlying the work on the development of the theory.

*Universitets Institut for teoretisk Fysik.*

Copenhagen, September 1922.

# ØKOLOGIENS GRUNDFORMER

UDKAST TIL EN SYSTEMATISK ORDNING

AF

EUG. WARMING

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D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATH. AFD., 8. RÆKKE, IV. 2.



KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL

BIANCO LUNOS BOGTRYKKERI

1923





## I.

I de seneste Aartier har Planternes Samfundslære i stærkt stigende Grad syslet bl. a. med den videnskabelige Forstaaelse af Sammenhængen mellem Samfundene selv og Standpladsernes Natur. Til Løsning af denne Opgave stiller hvert konkret Samfund (Association) følgende Krav: 1. Udarbejdelsen af en Flora, som omfatter saa vidt muligt alle, baade højere og lavere organiserede Arter. 2. En procentvis Redegørelse for de enkelte Arters Hyppighed, en Hyppighedsskala. 3. En indgaaende Undersøgelse af Standpladsens Natur, d. e. de paa Voksestedet herskende fysiske og kemiske Faktorer, hvad enten de stammer fra Livsrummet (Mediet) eller fra Klimaet (navnlig Varme og Nedbør) eller fra Jordbunden eller fra Samlivet med andre levende Væsener, d. e. Symbiosen i videste Forstand (Standplads, *Statio*, *Habitat*, *Standort*; se Beretningen om Kongressen i Bruxelles 1910). Naar Kaarene paa et Voksested forandrer sig, vil dette før eller senere, paa Grund af Samlivet mellem Arterne, der kan være hæmmende eller fremmende for den enkelte, give sig Udtryk i Samfundets Sammensætning; den maaske gennem Aarhundreder opnaaede Ligevægt mellem Arterne i Henseende til Hyppighed forandres (Sukcessionslæren). Her kan ogsaa mindes om Aarstids-Aspekterne. 4. Et indgaaende Studium af Samfundets Livsformer, d. e. Tilpassetheden af i første Linie de enkelte Arters Vegetationsorganer i Bygning og Liv til Standpladsens Kaar, eller deres Epharmoni (VESQUE) eller Økologi (HÄCKEL).

Den vanskeligste og største Opgave er at gøre Rede for de forskellige Arters Husholdning og dernæst ogsaa for deres Deltagelse i det hele Samfunds Husholdning. Hver Plantedel er et Redskab, som maa passe til sit Arbejde og til sine Omgivelser. Herved er at mærke, at »Livsform« ikke maa tages for tungt, som om der kun er Tale om det umiddelbart synlige, hvorved »Livsform« for en Del vilde blive Udtryk for »Fysiognomi«; ogsaa saadanne Livsytringer, der ikke er umiddelbart synlige, bør saa vidt muligt tages med i Betragtning. Fysiognomi og til Dels ogsaa Livsform har Menneskene for længe siden haft Øje for (f. Ex. stedsegrønne eller løvfældende Vedplanter, Græsformen og andre urteagtige Planter osv.). Men Livsformernes Epharmoni er endnu kun lidet studeret og kun lidet forstaaet. En umaadelig stor og vanskelig Opgave er her stillet os, nemlig Forstaaelsen af Stofskifteprocessernes Rolle for Samfundene.

Paavirket navnlig af IRMISCH gjaldt mine første Studier, for nu 5—6 Aartier siden, Blomsterplanternes Natur og Bygning. De var, ligesom hans, for en stor Del, rent morfologiske; Spørgsmaalet »Funktionen« traadte for meget eller helt i Baggrunden. En første Afhandling fik jeg 1884 trykt i »Naturhistorisk Forening«s Festskrift (»Om Skudbygning, Overvintring og Foryngelse«), vistnok det første Forsøg i Literaturen paa at give en mere indgaaende, samlet Oversigt over Blomsterplanternes Formtyper. Efter Tidens Aand var det et mere morfologisk Arbejde, end jeg nu maa sætte som Maal. Med store Afbrydelser har jeg fortsat disse Studier og lejlighedsvis publiceret en Del af dem, og naturligvis har en hel Del andre Botanikere i Aarenes Løb syslet med de samme Æmner, f. Ex. F. ARESCHOUG, O. DRUDE, C. RAUNKJÆR, BRUNDIN, SYLVÉN, MASSART o. a. Jeg forsøger nu her den vanskelige Opgave at give en systematisk ordnet Oversigt over Livsformerne, for om muligt at nærme os til et naturligt System af Vegetationsformerne og af Samfundene (»Plantesociologien«), d. e. Kausalsammenhængen mellem Arternes Standpladser og deres hele Epharmoni med disse.

Jeg undlader i foreliggende Oversigt at give Literaturhenvisninger. Mit Ønske er at fremstille et Udkast til en gennemført ny Ordning af »Livsformerne«, foreløbig i meget sammentrængt Form, men forhaabentlig efterfulgt af en større, med fyldige Literaturhenvisninger og Illustrationer forsynet, — om jeg skulde faa »Tid« dertil. Skulde dette, her foreliggende meget ufuldkomne, Udkast kunne hjælpe et lille Skridt fremad mod Opgavens Løsning, mod hvad der staar for mig som et i Planternes Samfundslære nødvendigt, men ogsaa meget vanskeligt Maal, vil jeg være tilfreds. De autøkologiske og synøkologiske Studier drives efter min Opfattelse endnu alt for ensidig og utilfredsstillende. I Virkeligheden frembyder allerede Opstillingen af et Livsformernes System store Vanskeligheder, efter min Mening navnlig følgende.

## II.

### Epharmoniske og indifferente Karakterer.

En systematisk Oversigt over Planterigets Livsformer bør bygges op paa alle for Livsførelsen væsentlige Ejendommeligheder. Men de er ikke alle lige vigtige. De bør altsaa deles i over- og underordnede, i de for Livet mest vigtige og de mindre vigtige. Men endnu formaar vi ikke at gennemskue Plantelivets Fænomener og Nyttens af de mange forskellige Bygningsforhold saa sikkert og indtrængende, som Opgaven fordrer. Fremtidige Livsform-Systemer vil sikkert komme til at bygge langt mere paa Stofskifteprocesserne i Planterne, paa Cellernes kemiske og fysiske Arbejder, altsaa paa de ikke umiddelbart synlige Egenskaber, end vi nu er i Stand til. Saa godt som muligt søger jeg at grunde et Livsformsystem paa, at Planterne, ligesom alle andre levende Væsener, stiller Krav til dagligt Brød, til en Bolig (Standplads, *ὄικος*), som passer for hver enkelt af dem i Henseende til Luft, Lys, Varme, Vand og andet for Livets Ophold nødvendigt, samt til passende

Klædning og Værktøj til det Arbejde, som de maa udføre for det individuelle Livs Opholdelse, men jeg maa gaa ud fra de ydre Former, hvorunder dette Arbejde aabenbarer sig.

Endvidere gaar jeg ud fra, at det er Individernes Husholdning (Arbejde), som det i første Række drejer sig om; medens Arternes Opholdelse, Formering og Vandring kommer i anden Række. Her møder os imidlertid mange Vanskeligheder, vor Forstaaelse af Epharmonien er endnu saa yderst ufuldkommen. Det er vanskeligt altid at skelne klart mellem de epharmoniske, og hvad jeg vil kalde de indifferente (»konstitutionelle«) Karakterer. Det er de epharmoniske, der bestemmer Livsformen; men de er i enhver Art kaleidoskopisk blandede med indifferente, som skyldes Slægtskab og kommer igen ofte hos mange forskellige Arter paa meget forskellige Standpladser og med meget forskellig Epharmoni, f. Ex. Bladformer og Nervation hos Græsser og mangfoldige andre Monokotyledoner, Bladformer hos Palmer og Cykadeer, osv. De indifferente Karakterer kan derimod have en meget fremtrædende fysiognomisk Betydning.

De indifferente Karakterer er i Regelen uforanderlig faste, medmindre sygelige Tilstande optræder; af de epharmoniske ændres nogle let, andre vanskelig og langsomt. Livsformerne maa til Dels opfattes som individuelle Tilstandsformer (Forsøg af BONNIER, VÖCHTING, GOEBEL o. a. har belært os om Arternes Plasticitet). De let foranderlige er vel i Regelen at opfatte som fylogenetisk yngre, de andre som fylogenetisk ældre, der gennem maaske uendelig lange Tidsrum har fæstnet deres Karakterer i Harmoni med uforandrede Kaar. (Om den arvelig faste Epharmoni er opstaaet ad Lamarckistisk Vej eller gennem Selektion af Mutanter eller paa anden Vis, er et Spørgsmaal for sig). At nye Egenskaber kan fremkomme korrelativt, altsaa indirekte som Følge af andre Egenskabers Fremkomst, bør ogsaa nævnes i denne Sammenhæng.

Den store Regulationsevne hos Planterne gør det endvidere ofte vanskeligt at genkende og bestemme Arterne. Hermed staar atter i Forbindelse, at alt bliver flydende, d. e. der mangler saa ofte skarpe Grænser mellem Livsformerne; i et »System« skal det helst være let at skille de forskellige Led fra hverandre, men her glider de ofte saa jævnt over i hverandre ved Mellemformer, saa at det personlige Skøn og den individuelle Opfattelse let kommer til at spille en altfor stor Rolle.

Ogsaa for selve Samfundsopfattelsen faar dette Betydning. Associationerne, d. e. de konkrete Samfund og ligesaa de enkelte Lag i dem, maa som anført grundes paa deres Livsformer. Men Associationerne bør, for at vi kan naa Overblik i Samfundslæren og give klare og overskuelige Fremstillinger af Landenes geobotaniske Natur, atter samles i »Formationer« eller hvad Navn man vil anvende, ligesom Systematikens Arter sammenstilles i Slægter. Det er da klart, at man maa tilstræbe de klareste Begrebsbestemmelser først og fremmest af Livsformerne og Associationerne.

Fra urgammel Tid har Menneskene dannet Navne for Planternes Grundformer (Træ, Busk, Urt, Mos osv.) saa vel som for en Række Samfundsformer



(Skov, Krat, Græsmark, Hede, Eng osv.). Herved har det Fysiognomiske spillet en meget væsentlig Rolle, og ogsaa i den ældre Plantegeografi, f. Ex. hos HUMBOLDT, spillede Fysiognomiet en stor Rolle. Der var endnu ikke Tale om at skelne mellem epharmoniske og indifferente eller systematiske Egenskaber. Mod denne Adskillelse er det, at Fremtiden maa stræbe hen; den maa lære at analysere »Fysiognomiet«. Vi maa da først og fremmest grunde Samfundslæren paa Livsformerne og tilstræbe at skelne mellem de epharmoniske og de indifferente Karakterer.

Der er andre og mindre Vanskeligheder for Opstillingen af et Livsformernes System, bl. a. at finde træffende og korte Benævnelser af de enkelte Livsformer. Fra ældre Tid har man nogle Navne og Signaturer, der mest drejer sig om Livsvarigheden; andre er senere føjet til (DRUDE, RAUNKLER, ENGLER, GAMS). Skønt jeg ingenlunde er glad ved den »Terminologitis«, som synes at grassere i vor Tid, har jeg dog følt det nødvendigt at danne nogle nye Termini.

Jeg tænker mig, at efterhaanden som Systemet grundigere udarbejdes, vil det blive praktisk at vælge visse Arter som Type for Livsformer — en Tanke, som jeg udtalte allerede 1884. Fordringerne maa da være, at disse Arter er almindelig kendte, derfor helst vidt udbredte; at deres Karakterer er lette at opfatte og udtrykke i Ord, paa samme Maade som VESQUE blandt Vand- og Sumpplanter skelner mellem typhoide, nymphoide, zosteroide o. a. Typer. Som Exempel kunde jeg tænke mig en *Taraxacum*-Type som Betegnelse for enhver urteagtig, fleraarig Art med semi-virent Helroset og kraftig Primrod; eller en *Solanum tuberosum*-Type som Betegnelse for en fleraarig, pseudoannuel Urt, der har Langskud og Jordudløbere med Ammeknolde. Jeg har gjort enkelte Forslag hertil i det her foreliggende Arbejde, men ikke gennemført Sagen.

### III.

## Økologiens Grundformer.

De vigtigste Karakterer synes mig at maatte hentes fra 1) Planternes daglige Ernæringsarbejde, 2) deres Vandøkonomi og 3) deres Epharmoni med Aars-tiderne, navnlig Overvintring eller Bortkastning af Assimilationsorganerne, det individuelle Livs Varighed, Overvintringsknoppens Natur, Redskaber for Oplagsnæring, Arbejdets Genoptagelse (Løvspring). Disse Forhold omtales i det nærmest følgende (S. 124—134). Skønt der er stor Forskel mellem Arterne i H. t. at taale forskellige Varmegrader eller til Aandedræt, faar dette dog ikke noget synligt Udtryk i Arbejdslivets Former, og maa derfor forbigaaes her.

#### 1. Det daglige Ernæringsarbejde. Kulsyre-Assimilationen.

Som det første store Skel mellem Livsformernes Husholdning maa jeg opstille Forskellen mellem autotrofe og alløtrofe (syn. heterotrofe) Arter. De første har Klorofyl og formaar ved dette og Lysets Hjælp at danne Kulhydrater af Luftens Kulsyre; alle andre (bortset fra nogle smaa Grupper af Bakterier) formaar

ikke dette; de er ikke grønne ved Klorofyl og maa, som Helsaprophyter eller Helparasiter, skaffe sig kulstofholdig Næring fra det organiske Stof, som andre Organismer allerede har tilberedt. (I det følgende forstaar jeg ved »Assimilation« Kulsyre-Assimilationen.)

Det klorofylholdige Redskab for Autotrofernes Assimilation kan kortelig og alment kaldes Assimilator, hvordan dets Form og Bygning end er. Forøvrigt er de jo meget forskellige: Thalli hos Thalloyter, Løvblade og Løvskud hos Kormofyter. Da Assimilationen er afhængig af Lyset, maa Assimilatorerne tilpasses til Belysningens Styrke og Retning, foruden naturligvis til Livsrummet (Luft, Vand). En stor Mængde speciellere Former for Assimilatorer fremkommer herved. Nærmere at gaa ind paa deres Anatomi og Epharmoni paa dette Sted maa være overflødigt.

Allotroferne har altsaa ingen grønne Assimilatorer; naar de sender Legemsdele ud i Lyset, uden for Substratet, er det for Forplantningens, Formeringens og Vandringens Skyld. Allotroferne maa opfattes som yngre Typer, der er spredte om i Planterigets forskellige Nedstammingslinier, og de forenes derfor her i en egen Række, i Systemets allersidste.

Allerede her kan talrige Mellemløper nævnes, Mixotroferne (PFEFFER), d. e. klorofylholdige, derfor autotrofe Arter, der tillige lever allotrofisk af organisk Næring (Halvsaprophyter, Halvparasiter o. fl.). Da de ligesom Autotroferne har grønne Assimilatorer, der maa tilpasses til Lyset, maa de i Systemet anbringes mellem Autotroferne, de mest afvigende i særlige Grupper.

Assimilatorernes Hovedformer hos Kormofyterne bør nævnes allerede her, fordi de straks benyttes af mig til Inddeling inden for de enkelte Klasser. I øvrigt synes de i Almindelighed mere at være arvelig indifferente end epharmoniske Former. Thalloyternes Assimilatorer nævnes bedst under de enkelte Klasser.

Kormofyternes Skud deles saaledes:

- A. Oprette (orthotrope). Hovedaksen opret, Sideakserne mere eller mindre skraat udgaaende. De er 1) Langskud, som er enten langeddede eller kortleddede og i dette Tilfælde oftest har smaa, linie- eller skælfornede Blade, 2) Rosetskud, der atter deles i Hel- og Halvrosetskud.

#### AA. Nedliggende (plagiotrope).

De oprette Skudformer bliver Grundlag ogsaa for nogle fysiognomisk forskellige Former, der benævnes Tueplanter (*plantæ caespitosa*), Pudeplanter (*pl. pulvinatæ*), og som sædvanligvis er udpræget epharmoniske Typer.

Af disse Livsformer med oprette Skud er mange i overvejende Grad stavnsbundne (stedbundne; WARMING 1884); andre har vegetativ Vandring ved nedliggende og rodslaaende Skud, »Vandreskud«.

De er endvidere for allerstørste Delen autonome eller selvstændige, d. e. deres Stængler og Grene holder sig oprette og i Stilling ved egen Kraft, enten ved Saftspænding (turgor) eller ved Forvedning eller ved begge Midler. Anordningen af de mekaniske Væv sker som bekendt efter mekaniske Principer (SCHWENDENER).

Vi har da straks her Modsætningen mellem Urter (*herbæ*) og Vedplanter (*pl. lignosæ*) og Mellemformerne (*sublignosæ*).

Mellem de autonome Vedplanter træffes nogle velbekendte fysiognomiske Typer: Træformen og Buskformen med mange forskellige Højder. Det er de oprette Assimilatorer, der bedst præger Vegetationens Fysiognomi.

I Modsætning til de autonome staar de uselvstændige, Klatreplanterne (*pl. scandentes*; Klasse 15), hvis Assimilatorer ikke er i Stand til at holde sig oprette ved egen Kraft, selv om Stænglerne er stærkt forveddede, men som enten ved ejendommelige Redskaber eller Omslyngning af Støtter maa søge at komme op til Lyset.

En helt afvigende Type af Assimilatorer er de plagiotrope, der findes baade hos Thalloyter og Kormofyter, hos Vandplanter og Landplanter, hos Urter og Vedplanter. Deres Akser lægger sig ned paa Jorden eller trykker sig op til skraa eller endog lodrette Flader, idet de bliver dorsiventrals; naar de hæfter sig til disse ved Rødder eller paa andre Maader, kan de optræde som sociale Arter, der danner Tæpper eller Maatter. Følgende Trin eller Under typer findes:

a. Nedliggende (*prostrate*). Disse udgaar fra oprette Assimilatorer, er nedliggende, men ikke rodslaaende. Vegetativ Vandring finder derfor ikke Sted, saaledes som hos de følgende kan være Tilfældet.

b. Lysudløbere (*stolones*). De nedliggende Skud udgaar ogsaa her fra Basis af oprette Skud, men er rodslaaende, kan derfor danne Aflæggere; Arten kan vandre ved dem. Lysudløberne kan have forskellig Form, f. Ex. være Flagella.

c. Krybplanter (*pl. repentes*). Assimilatorerne er nedliggende og rodslaaende, men udgaar ikke fra Grunden af oprette Skud; de dør efterhaanden bort bagtil, medens Forenden vokser videre. Forøvrigt kan de have meget forskellig Form (f. Ex. være gaffelgrenede, thalløse eller bladbærende); nogle er bundne til vandrette Flader, andre til skraa eller lodrette.

d. Som et Slutningsled kan den skorpeformede Assimilator nævnes, der findes f. Ex. hos nogle Alger, Likener og Podostemaceer.

De plagiotrope Assimilatorer viser forskellig Tilpassethed til de ensidig virkende Kræfter (Lys, Tyngde). Bl. a. er Dorsiventralitet og Mosaikdannelse almindelig,

**Mellemstok (mesocormus).** Flere af Typerne med oprette (autonome eller klatrende Skud, Tueplanter, Pudeplanter) grener sig fortrinvis tæt ved Jorden eller i selve Jordskorpen (buskformet). Dette nederste grenede Parti fortjener et eget Navn, især fordi det hos de mange fleraarige Urter eller Sublignoser kommer til at udskille sig paa særlig Maade fra Plantens overjordiske Assimilator-Dele, naar disse nemlig ved Vegetationstidens Slutning afkastes. Som en Slags Stub staar da de nederste Skudrester tilbage, lige over Jorden eller endog noget skjult i Jordskorpen (hemigeofytisk). Dette Skudparti bliver ofte kaldt »Rodstok«, hvilket absolut maa misbilliges, da dette Navn har og bør have en helt anden og rigtigere Anvendelse (om underjordiske, vandrette, næringsrige, særlig kortleddede og hologeofytiske



Skud), Man finder imidlertid i Literaturen ogsaa det fortræffelige Navn »Mellemstok«, d. e. det mellem Rod og »Krone« liggende Skudparti, og dette Navn bør bevares. Undertiden udvikles det paa en særlig Maade til et forveddet, haardt, tykt, mangeaarigt Legeme, som kan være Bærer af mange urteagtige eller forveddede Skud i Tueform, et »Xylopodium« (C. LINDMAN); det træffes særlig i Steppe- og Ørkenegne. Ligeledes synes de tykke, næringsrige og bløde (»kødfulde«) Skudformer, som almindelig kaldes Knold eller Løg, i mange Tilfælde passende begrebsmæssig at kunne slutes til Mellemstokkene.

## 2. Vandøkonomien.

Som den Faktor, der næst Kulsyre-Assimilationen præger Livsformerne mest, vil jeg nævne Vandet, ved hvis Hjælp mineralske Næringsstoffer optages og ledes omkring i Plantelegemet. Størrelsen af Indtægten og Udgiften af Vand under det daglige Ernæringsarbejde er af allerstørste Betydning for Plantens Trivsel, Vækst og Bygning. Her møder os straks Skellet mellem de to store Grupper af Livsformer: Vandplanter (Hydatofyter) og Luftplanter (Aërofyter); deres Assimilatorer er grundforskellige baade i Henseende til Optagelsen og Ledningen og Afgiften af Vand.

Vandplanterne er submerse og kan i det store Hele optage Vand gennem Legemets hele Overflade; de behøver derfor næsten ikke og har næsten heller ikke Veje anlagte til Ledning af Vand. Vævene er overordentlig lidet differentierede, og Tykkelsevækst findes ikke. For dem er der heller ikke Tale om egentlig Fordampning og Regulering af en saadan.

Luftplanterne er paa ethvert Punkt forskellige fra dem, hvad ikke nærmere kan omtales her. For deres Vedkommende er vi for længe siden ført til at skelne mellem 1) Hygrofyter, der er knyttede til en meget fugtig Luft, og undertiden, efter hvad der angives, kan optage Vand fra Vanddampene i denne; 2) Xerofyter, der er tilpassede til ringe Vandforbrug og til længe at udholde stærk Fordampning, fremkaldt ved Tørhed i Luften eller stærk Blæst, eller Mangel paa Vand i Underlaget, og 3) Mesofyter, der passer bedst til Middelforhold baade i den ene og den anden Henseende. Selvfølgelig er der ingen skarpe Grænser mellem disse Begreber. Hvorvidt en Plante hører til den ene eller den anden Type, kan iøvrigt ikke med Sikkerhed udledes af Form- og Bygningsforholdene, men maa afgøres ved Forsøg.

Ved Siden af de nævnte Assimilatorer maa opstilles to særlige Klasser af Livsformer, nemlig de, der anlægger store Vandoplæg i Blade eller Stængler, som derfor bliver kødfulde: Saftplanter (Sukkulenter, Bladsukkulenter og Stængelsukkulenter, SCHIMPER'S Chylofyller og Chylokauler). Aarsagerne til denne Ejendommelighed i deres Vandøkonomi er forskellige og vel næppe fysiologisk helt forstaaede; den ene Klasse er knyttet til arid Natur med stærk Lufttørhed og vandfattig Bund, saasom Sandbund, Klippebund og anden fast Bund, som Træstammer og lign., og kan i alt Fald foreløbig kaldes Eu-Xerofyter; den anden Klasse er

knyttet til saltholdig Bund: Saltbundsplanter (Halofyter). I mange Tilfælde er begge Faktorer forenede: saltholdig Bund med aridt Klima.

Fysisk tør kaldte SCHIMPER den Bund, der kun indeholder lidt Vand; fysiologisk tør den, der kan være endog meget vandrig, men af en eller anden Grund gør Vandoptagelse vanskelig (ved Salt, Syrer, Kulde o. a.). I begge Tilfælde tilpasses Fordampningen i Harmoni med Vandoptagelsens Lethed.

Vandoptagelse og Vandafgift er for de forskellige Arter reguleret paa meget forskellig Maade til det daglige Ernæringsarbejde i Arbejdstiden, samt under mere extreme Former til Arbejdet i Hviletiderne, altsaa til Periodiciteten i Naturen.

### 3. Epharmoni med Aarstidernes Fænomener. Periodiciteten.

Der er vist yderlig faa Egne paa Jorden, som Aaret rundt har fuldkommen samme Varme, Nedbør, Fordampning, Lys og andre Kaar (naturligvis bortset fra Forskellen mellem Dag og Nat). Selv i de tropiske Regnskove maa det vel betragtes som sjældent, at der findes Arter, som fortsætter Ernæringsarbejdet med uforandret Styrke gennem alle Aarets tolv Maaneder. I de allerfleste af Jordens Egne er der meget store Forskelligheder, som fra Planternes Side kræver tilsvarende Tilpasning, en ofte skarp Modsætning mellem en Arbejdstid og en Hviletid. Periodiciteten ytrer sig i Planteriget navnlig i følgende Retninger:

1. Overvintring. Bortkastning af Assimilatorer i Hviletiden (Løvfald). Det individuelle Livs Varighed.

2. Uddannelse af Beskyttelsesmidler mod Hviletidens Ugunst.

3. Oplagring af Næring til Brug ved Livets Foryngelse.

Om Hviletiden og dens Fænomener er en direkte Virkning af de ydre Kaar (er »induceret«), eller om de er autonome, kan ikke komme nærmere paa Tale her; ej heller den Forskel, der kan være i Henseende til Hvilens Natur.

**Bortkastning af Assimilationsorganer.** Der er Planter, selv Urter, som *Urtica dioeca*, *Euphorbia cyparissias*, *Amarantus retroflexus* o. a., der i Vegetationstiden bortkaster Løvblade; disse er Arbejdere, der er udslidte, ældede i Tjenesten og nu faar Afsked. Noget andet er det Løvfald, som staar i Forbindelse med Skifte i Aarstidernes Kaar, særlig Formindskelse i Vandoptagelsen, f. Ex. derved, at Jorden bliver kold. Her maa der skelnes mellem:

1. Stedsegrønne Arter (Sempervirente, SCHOUW 1821). Assimilatorerne varer over 12 Maaneder. De er derfor sædvanligvis xeromorfe eller sarkomorfe, fordi de maa være i Harmoni med alle Aarets Omskiftelser.

2. Løvskeftende Arter (Tropofile, SCHIMPER), som i den ugunstige Aarstid bortkaster alle de egentlig assimilerende Organer, som bekendt Løvbladene hos Vedplanter, hele Skud eller endog alt det overjordiske hos mange Urter (Hologeofyterne). Assimilatorerne er her mere eller mindre mesomorfe, fordi de kun er tilpassede til Arbejde i den gunstige Aarstid. De benævnes ofte »sommergrønne«.

3. Halvgrønne (Semivirente) foreslaar jeg at kalde de Arter, hvis Assimilatorers ældre Dele, navnlig Blade, dør bort, medens de yngste, endnu ikke udviklede, kan ses Vinteren igennem i Assimilatorernes (Skuddenes) Spids, omgivne af og utvivlsomt mere eller mindre beskyttede af nogle ældre og Rester af saadanne. Der er i vor Natur en Mængde halvgrønne Urter, og efter Vinterens mere eller mindre ødelæggende Natur overvintrer de mere eller mindre grønne. Denne Forskel i Løvbladens Varighed er en Epharmoni med Klimaet, og Arter, der paa en Lokalitet er semivirente, kan maaske paa en anden være løvfældende eller stedsegrønne. Ogsaa disse Arters Assimilatorer er oftest mesomorfe, nogle er dog sukku-lente (de halofile).

Til de tropofile hører som bekendt de allerfleste af det koldttemperede Klimas Løvtræer, og desuden en Mængde Urter. Mellemstokkene af mange fleraarige Urter bliver, som foran nævnt, som en Slags Stub staaende i større eller ringere Højde over Jorden og bærer her Foryngelsesknopperne, efter at den øvre Del er visnet; disse Arter vil kunne benævnes Hemigeofyter, idet Navnet »Geofyt« benyttes i den Betydning, som ARESCHOUG gav det 1896. Fra dem er der jævne Overgange til sublignose Planter, hvis Mellemstokke er højere og mere forveddede.

Hos andre urteagtige Planter dør Skuddene bort i hele deres Udstrækning over Jorden, og kun de allernederste i Jorden gemte Dele bliver levende tilbage som Bærere for Foryngelsesknopperne. Disse Arter kan kaldes Hologeofyter<sup>1)</sup>. Ved den gunstige Aarstids Begyndelse kommer nye Assimilatorer til Syne over Jorden. Arten er rediviv (renascent).

De i Jorden overvintrende Skud har som bekendt meget forskellig Bygning, hvorom i det følgende. Hviletiden falder forøvrigt selv i den samme Natur til meget forskellig Aarstid for de forskellige Arter. Disses Egennatur gør sig gældende. *Ficaria verna* gaar hos os til Hvile i Juni, og allerede i September findes Individuer med helt udviklede nye Rødder. *Anemone nemorosa* kommer noget senere. Mange andre Arters Arbejdstid ligger langt senere, og Hviletiden falder om Vinteren. Hvor-paa de Forskelligheder i Stofskiftet, som fremkalder disse i det ydre fremtrædende Forskelligheder, beror, er ikke opklaret.

**Det individuelle Livs Varighed.** Det individuelle Livs Varighed har stor Betydning for Livsformen og for Samfundenes Sammensætning og sociale Liv. Den afhænger for det første i høj Grad af Stofskifteprocesserne, som usynlig foregaar i Plantens Indre, og før eller senere ufejlbarlig ender den med Døden. Hvordan det gaar til, at Livet efterhaanden ebber ud, og Forplantningen i mange Tilfælde øjensynlig sætter en brat Afslutning, f. Ex. hos de hapaxanthe Arter, og det selv i Algeverdenen, hvis ydre Kaar synes næsten ens Aaret rundt, forstaar vi endnu ikke. Ej heller kan vi gøre fuld Rede for Forstærkningstiderne, d. e. de vegetative Tidsrum, som med meget forskellig Længde gaar forud for den første (sexuelle)

<sup>1)</sup> RAUNKJÆR har dannet Navnet Hemikryptofyt, men han indbefatter under Navnet Kryptofyt ikke blot Geofyter, men ogsaa Vand- og Sumpplanter.



Forplantning, og som ligeledes optræder senere med meget forskellig Længde hos de enkelte Arter mellem Forplantningsperioderne.

Livets Varighed har imidlertid stor Betydning som Inddelingsprincip i et Livsform-System, og i mange Tilfælde staar den ogsaa tydelig i Harmoni med Kaarene. I det følgende skelner jeg mellem følgende Trin:

A. Hapaxanther (AL. BRAUN). (Monokarpiske Planter DE CAND.). — Individet dør efter første Frugtsætning og formerer sig kun ved Frø eller lignende Organer. De er:

1. Sommerannuelle. Lever kun i een Vegetationsperiode, d. e. een gunstig Aarstid, og dør derpaa. De er »monocykliske« (☉), og i Harmoni hermed findes mest Langskud hos Kormofyterne. — Efemer kaldes en Plante, der i særlig kort Tid tilendebringer Livets Løb, f. Ex. faa Uger, og maaske kan sætte Frugt flere Gange i samme Vegetationsperiode.

2. Vinterannuelle (*Pl. annuæ hiemantes*). Spirer om Efteraaret, afslutter Livet næste Foraar. »Dicykliske« (☉). Assimilatorerne har ofte Roset i Harmoni med, at Væksten ikke er lige stærk til enhver Tid.

3. Bienne Arter; to-aarige. Livet er ogsaa her fordelt paa to Arbejdsperioder med en mellemliggende, af ugunstige Kaar betinget Hviletid, men Forstærknings-tiden er længere; Spiringen sker om Foraaret, Frugtsætning næste Aars Efteraar, altsaa efter mere end 12 Maaneders Forløb. Ofte henlægges Oplagsnæring for Frugtsætningens Skyld. Er ogsaa dicykliske (☉☉), og Skuddene har Roset.

4. Plurienne-Hapaxanther. Forstærkningstiden udstrækkes over to til flere Aar. »Pleioicykliske« eller »polycykliske« Arter (☉—☉); Skuddenes Roset-form er endnu mere udpræget i Harmoni med den længere varende Forstærkningstid. Undertiden megen Oplagsnæring i Rødder og Mellemstok.

Hapaxantherne er næsten alle Urter; kun faa Vedplanter findes (nogle Palmer, Bambus samt Agaver, *Musa Ensete*).

RAUNKIÆR sammenfatter Sommerannuelle og Vinterannuelle under en fælles Betegnelse: Therofyter.

AA. Pollakanther (KJELLMAN). Perennerende Arter. — Forstærkningstiderne er flere i Antal og varer ofte flere Aar; de enkelte Individuer kan i Livets Løb forplante sig (sætte Frugt) flere Gange. Mange har ogsaa vegetativ Formering. Nogle er Vedplanter, andre Urter, der i det daglige Liv ofte kaldes »Stauder«.

Da Livsvarigheden ikke blot afhænger af arvelige Karakterer, men ogsaa af Livskaarene, er det naturligt, at mange Arters Livsvarighed i høj Grad er varierende (HILDEBRAND, K. JOHANSSON). Den er for mange Arter en epharmonisk og foranderlig Karakter. Livet kan forlænges, naar Blomstring hindres.

**Hvile- og Foryngelsesknopperne.** RAUNKIÆR bygger sit Livsform-System først og fremmest paa Pladsen for og Naturen af Hvile- og Foryngelsesknopperne og Maaderne, paa hvilke de Knopper bevares, der skal føre Assimilatorerne eller Planterne i det hele uskadte gennem den ugunstige Aarstid. Dette er ogsaa en meget vigtig

Sag, som f. Ex. ogsaa DRUDE har betonet (1890). At de alleryngste Skudspidser (Vækstpunkterne, de embryonale Væv) særlig maa værnes mod Indtørring ved Fordampning og andre Farer, er klart. Dette gælder da iøvrigt ikke blot for den ugunstige Aarstid, men ogsaa for selve Arbejdstiden. De Maader, paa hvilke Planterne realiserer dette, er for længst undersøgt og beskrevet af mange Forskere (i nyere Tid af PERCY GROOM og RAUNKLER).

Det er ved Rester af gamle Blade, ved Akselblade og Bladskeder, ved tørre, ofte med Kork og Harpiks o. a. forsynede særlige Dækblade, Knopskællene osv., hvis Rande lukker sig tæt over hverandre og de yngste Anlæg, at Beskyttelsen udføres. De tropiske Vedplanters Hvileknopper er som Regel ikke saa store, som de koldtempererede Egenes, hvilket aabenbart maa sættes i Forbindelse med, at deres Hviletid er kortere og Arbejdstiden meget længere, hvorfor de ikke behøver at indeholde saa megen Oplagsnæring samt saa mange Blad- og Blomsteranlæg, som de koldtempererede Egenes. I disse er Arbejdstiden derimod saa kort, at mange Organer maa anlægges Aaret før Løvspringet og en større Mængde Oplagsnæring samles.

Underjordiske Knopper er altid udstyrede med Knopskæl, da de skal hvile i og gennembore Jorden. Saavel over som under Jorden kan findes Knopper, der maa opfattes som Reserveknopper.

**Oplagsnæring.** I nøje indre Sammenhæng med Periodiciteten (»ugunstig Aarstid« og »helt Løvsifte«) staar Henlæggelsen af Næring og Vand (Oplagsnæring) til Brug for den første Organdannelse (Dannelsen af nye Assimilatorer, Blomster m. m.), naar Arbejdet genoptages i den nye Vækstperiode. Oplagsnæringen henlægges i Parenkymceller. Nogle Oplagsorganer er varige, d. e. de kan benyttes Aar efter Aar eller dog gennem flere Aar (Stængler og Rødder af Vedplanter, mange Knolde, Løvblade hos mange Saftplanter o. a.). Andre varer langt kortere Tid, nogle er endog enaarige, idet de udnyttes helt ved den nye Arbejdstids Begyndelse. De kortvarige kan benævnes Ammeorganer. Arter, hvis Individer gaar helt til Grunde under Hviletiden saaledes, at kun Foryngelsesknopperne med deres Oplagsnæring eller andre Indretninger til selvstændig Genoptagelse af Arbejdet bliver tilbage, betegnes bedst Pseudoannuelle, et Navn, der vist er indført af BAILEY (f. Ex. *Solanum tuberosum*, *Epilobium montanum*, Arter af *Potamogeton*, *Ophrydeæ*, *Samolus Valerandi* og andre).

Hos mange bruges ikke al Næring i hver Arbejdsperiode; nogen bliver undertiden tilbage til et følgende Aar; Arten har en »Sparekasse« for Ulykkestilfælde (OLTMANN).

De almindelige Organer for Oplagsnæring omtales i alle Lærebøger (Knoldrødder, Knoldstængler, Løg). Hertil kan føjes: Mellemstokkene med Xylodierne, og forøvrigt alle underjordiske Skudformer (»Geoblaster«) og Rødderne.

Underjordiske (subterrane, hypogeiske) Skud, Geoblasterne hos Holo-Geofyterne. Ligesom de supterrane assimilerende Skud kan de subterrane (eller

hypogeiske) Skud deles i orthotrope og plagiotrope. De orthotrope har væsentlig kun den Opgave at gemme Oplagsnæring, og ved Rodkontraktion eller paa anden Maade føres de ned til en vis Dybde i Jorden (ROYER's: Loi de niveau). Rodkontraktion, som i nyere Tid navnlig RIMBACH har studeret, forekommer hos en Mængde Urter (Hemi- og Hologeofyter). Den fører Stænglerne ned til nogenlunde bestemt Dybde; jo dybere de kommer i Jorden, med desto mere Næring udrustes de da i Regelen. De plagiotrope er mere eller mindre vandrette og kan paa andre Maader søge og finde Plads i Jorden i en vis Dybde (WARMING 1918). Deres Opgaver er forskellige: at fæste Planten i Jorden, gemme Oplagsnæring og sørge for Plantens (d. e. Artens) Vandring. Herefter tilpasses de paa forskellig Vis. De særlige Vandreskud er tynde og langledede; de, der særlig gemmer Oplagsnæring, er kortledede og tykke (kødfulde). Selvfølgelig er der Mellemløbere, der binder dem sammen; mellem kort og lang, tynd og tyk lader sig ikke opstille skarpe Grænser.

Jeg ordner dem paa følgende Maade:

A. Lang- og tyndledede plagiotrope Skud er særlig Vandreskud, hvis vigtigste Egenskaber fremmer Artens Udbredelse. Jo mere grenede de er, desto mere samlagdannende vil de være. Arter som *Paris quadrifolia*, *Listera ovata* danner vanskeligt tætte Samlag.

B. Jordudløbere (Soboles). Grendannelsen er uregelmæssig, der er ingen til nogen bestemt Bladaksel knyttet Hovedknop (Kraftknop); f. Ex. *Equisetum*, *Phragmites* og mange andre Poioider (WARMING 1918).

BB. Rhizoder (WARMING 1918). Der er en lovbestemt Arkitektonik i Skuddenes Grening, med en til bestemt Bladaksel knyttet Hoved- eller Kraftknop (ῥιζωδης, rodliggende); Ex.: *Juncus balticus*, *Heleocharis palustris*, *Scirpus lacustris*. (Der synes ikke at findes Rhizoder over Jorden.)

AA. Rodstokke (Rhizomata). Skuddene er plagiotrope, oftest kortledede, tykke (næringsrige). Ofte bestemt Arkitektonik med pladsbestemt Kraftknop. Ofte er de udpræget dorsiventrale, og kan være afdelte i knoldformede Stykker. (Ex.: *Polygonatum*, *Iris*, *Asparagus officinalis*, flere *Araceer*). Navnet »Rhizom« bruges desværre meget ubestemt og overfladisk; man kan finde dette Navn anvendt til Betegnelse af baade over- og underjordiske Grundakser, baade Mellemskud og Udløbere, og næsten om enhver i Jorden eller endog paa Jorden liggende Stængel, der ikke netop er Knold eller Løg. De underjordiske Stænglers biologiske Betydning er imidlertid ret forskellig, og dette bør fastslaaes gennem forskellige Navne, selv om Overgangsformer kan volde Vanskeligheder for Anvendelsen i Praxis.

En noget afvigende Form af Jordskud er de Løvblad-Rhizomer (WARMING 1918), som findes hos visse Arter: Kryb-Skud, der ligger oftest meget højt i selve Jorden, og som er assimilerende, da de bærer Løvblade. Hos mange Bregner findes saadanne, bl. a. *Polypodium vulgare*, og paa Grund af Bladenes ejendommelige Vækstforhold hos Bregnerne kan Stænglerne ligge endog ret dybt i Jorden, som f. Ex. hos Ørnebregnen. Herhen ogsaa en Del Blomsterplanter, saasom *Oxalis acetosella*, *Aspidistra*, *Butomus*, *Iris*, *Zostera* o. a. De har, saa vidt jeg har set, ikke Stængel-



ender, der er spidse og derved let kan gennembore Jorden, men har butte, undertiden ligefrem afrundede Stængelender.

**Dybdelejets Nytte.** Den Nytte, som Planterne har af at gemme saa mange Organer mere eller mindre dybt i Jorden, er utvivlsomt forskellig. For det første Beskyttelse mod Klimaets Ugunst, men for de mange Arter, der vokser i Skovbunden, endog i Tropeskovenes Muldbund, altsaa under de gunstigst mulige Kaar, synes dette Hensyn ikke at veje stort. Det samme synes at gælde for vore Skoves Muldbund, i hvilke en Mængde Geofyter har Leje i større eller mindre Dybde. Langt mere taler for, at disse næringsrige Plantedele ofte ved at gemmes i Jorden unddrages Dyrenes Efterstræbelser. Det vides jo, f. Ex., at Hjortene i vore Skove opgraver Rodstokkene af visse Skovbundsplanter, bl. a. *Dentaria*, for at fortære dem. Fra Sydafrikas mere ørkenagtige Egne har MARLOTH flere Exempler paa det samme; mange Knold- og Løgplanter er saa rige paa Næring, at de ivrig efterstræbes af Dyrene, især Bavianer; nogle spises ogsaa af de Indfødte.

Til de subterrane Vandrestængler slutter sig med væsentlige Afvigelser de »Rodskud« dannende Rødder; nogle spiller ganske Jordudløberes Rolle, f. Ex. hos *Cirsium arvense*, *Pirola uniflora*, *Chamaenerium angustifolium* o. a.

Alle Skud, som maa gennembryde Jorden for at komme op til Lyset, maa have deres Spids indrettet hertil. Dette sker paa noget forskellig Vis, hvad jeg nærmere omtalte for faa Aar siden (1918).

**Arbejdets Genoptagelse. Løvspringet.** Fuldstændig Bortkastning af Assimilatorer kræver Udvikling af helt nye. Hos alle Arter, hos hvilke Aarstidernes Skifte ledsages af en brat, hel eller delvis Bortkastning af Assimilatorerne, findes en tilsvarende brat Forryngelse med Udvikling af nye, et Løvspring. Ja, selv hos de stedsegrønne Vedplanter, hos hvilke en længere Standsning af Arbejdet forekommer, vil et saadant finde Sted, og dette ej blot f. Ex. i vort koldtempererede Klima (vore Naaletræer, *Ilex* o. a.), men ogsaa i Troperne (se f. Ex. WARMING: Lagoa Santa). Undtages maa dog visse Tropeplanter, f. Ex. Palmer, der jævnt gennem hele Aaret udvikler nye Blade.

Af Aarsskudene er nogle ugrenede, andre grenede, og det ikke blot hos Urter, men ogsaa hos Vedplanter. Dannelsen af »Sommerskud« og i det hele Grening af Aarsskud synes at afhænge af Ernæringens og Vandtilførselens Rigelighed. Mange Knopper bør nærmest betragtes som Reserveknopper i Husholdningen.

### Karakterer af ringere Orden.

I det foregaaende er nævnt de Livs- og Bygningsforhold, der maa anses som de vigtigste til en systematisk Opstilling af Økologiens Livsformer. Der er en stor Mængde andre, som jeg, i alt Fald foreløbig, af forskellige Grunde maa sætte i 2den Række, nogle maaske, fordi vi endnu ikke kender deres virkelige biologiske Betydning, f. Ex. monopodial og sympodial Grening, Forskellen i Bladlejet, Mælkesaft, Anthokyan; andre, fordi de kun findes saa spredt, kun hos faa Arter, der

lever under særlige Kaar, til hvilke de maaske tydelig nok er tilpassede, saasom Aanderødder, Brændehaar, Kauliflori o. a.; eller modsat, fordi de aabenbart er indifferente, rent systematiske Bygningsforhold, som genfindes hos andre Arter i samme Slægtskabsomraader, selv om de vokser under yderst forskellige Kaar og biologisk og økologisk er meget forskellige indbyrdes, f. Ex. bestemte Bladstillinger, visse Greningsmaader o. a.; eller endelig, fordi det mindre er for Individernes Ernæringsliv end for Arternes Formering og Vandring, (bl. a. Bulbiller, Frødannelse), at de er nyttige. Som alt bemærket hører Vandringsskud, hvad enten de er subterrane eller supraterrane, Yngleknopper og lign., til denne sidste Gruppe. Idet jeg i det følgende ordner Livsformerne indenfor de forskellige Klasser i en vis Rækkefølge, sætter jeg, saa vidt det findes praktisk, Vandringsskuddene efter de stavnsbundne, men i øvrigt nærstaaende Typer.

#### IV.

### Oversigt over Livsformernes Ordning.

Paa Grundlag af den i det foregaaende givne Fremstilling ordner jeg her Livsformerne paa følgende Maade:

#### 1. Række. Autotrofer.

##### 1. Underrække. Vandplanter; Hydatofyter.

Submerse Planter, der optager Vand gennem Assimilatorernes hele Overflade. Ingen Fordampning.

Vandplanterne deles efter Maaden, paa hvilken de er fasthæftede i Forhold til Bundens Natur, i 7 Klasser, nemlig saaledes:

- A. Liberæ: frit levende, ikke fasthæftede..... Planofyter.
  - B. Svævende, nedsænkede i Vandet. Svæv,
    - Plankton..... 1. Klasse. Smaa-Svæv; Mikro-Plankton.
    - 2. Klasse. Stor-Svæv; Mega-Plankton.
  - BB. Flydende paa Vandet (fluitantes). 3. Klasse. Flydeplanter; Pleuston.
- AA. Bundfæstede, affixæ ..... Benthos.
  - B. Bunden blød (Dynd, Sand, Ler og lign.).
    - C. Planterne løst liggende, fæstede f. Ex. med Slimskeder og lign. til Bunden af Vandet.
      - Krybende ..... 4. Klasse. Herpo-Benthos.
    - CC. Planterne forankrede ved grenede Traade (Rhizoider, Rødder), der trænger ned i Bunden mellem dens mineralske Korn.
      - 5. Klasse. Rhizo-Benthos.

- BB. Bunden haard eller dog fast sammenhængende.  
 C. Planterne fæstede uden paa Underlaget  
 (Epilither, Epifyter) ..... 6. Klasse. **Hapto-Benthos.**  
 CC. Planterne tager Ophold inde i Under-  
 laget ..... 7. Klasse. **Endo-Benthos.**

## 2. Underrække. **Luftplanter (Aërofyter).**

Vandoptagelse enten fra Luftens Vand eller fra Jorden. Har Fordampning og Afhængighed af Klimafaktorer.

- A. Selvstændige (autonome); holder sig oppe og  
 i Stilling ved egen Kraft alene.  
 B. Epifytoïder. Aërisk Vand (Regn, Dug, Taage)  
 er eneste eller væsentligste Kilde til Vandet, som  
 optages gennem Assimilatorerne. Bunden er  
 fysisk tør. (**Epifyter, Epilither.**)  
 C. Vandet optages gennem Assimilatorernes  
 hele Overflade ..... 8. Klasse. **Atmofyter.**  
 CC. Vandet er væsentlig Regnvand, som op-  
 tages gennem Rødder eller andre særlige,  
 begrænsede Dele af Legemet og til Dels  
 oplagres paa forskellig Vis... 9. Klasse. **Ombrofyter.**  
 BB. **Chthonofyter.** Terrestrisk Vand; Vandet  
 optages gennem Rødder fra Jorden.  
 C. Planterne er af forskellig Grund hindrede  
 i at optage meget Vand.  
 D. Jorden er fysisk tør, haard (Sten,  
 Træstammer) eller anden for Rødder  
 vanskelig gennemtrængelig Bund eller  
 paa anden Vis som Regel stadig vand-  
 fattig Bund ..... 10. Klasse. **Saftplanter; Chylofyter.**  
 DD. Jorden er mere eller mindre porøs og  
 vandholdig, men fysiologisk tør:  
 Saltbund ..... 11. Klasse. **Saltbundsplanter; Halofyter.**  
 Herhen maaske ogsaa anden Art  
 af fysiologisk tør Bund. (Sur Bund,  
 Tørbund, kold Bund). I Literatu-  
 ren omtales f. Ex. **Oxylofyter.**  
 CC. Almindelig porøs Jord med Ferskvand og  
 Luft mellem de mineralske Smaadele, ikke  
 fysiologisk tør og ikke uden til visse Aars-  
 tider mere eller mindre fysisk tør. (Almin-  
 delig Agerjord, Havejord, Sandjord o. a.).



- D. Urter (*Herbæ, pl. herbaceæ*).  
 E. Mere eller mindre bredbladede  
 (ikke græsagtige) Urter.  
 12. Klasse. **Agrofyter.**  
 EE. Graminoïde Urter; Bladene lange,  
 smalle, ligenervede. 13. Klasse. **Græsagtige Planter; Poioïder.**  
 DD. Forveddede Stængler (Vedplanter; Lignosæ og Sublignosæ . . . . 14. Klasse. **Vedplanter; Xyloïder.**  
 AA. Uselvstændige. Urter og Vedplanter, der maa  
 have Støtte for at komme op i Vejret, op til Lyset.  
 Bunden er som hos Agrofyterne . . . . 15. Klasse. **Klatreplanter; Klinofyter.**

## 2. Række. Allotrofer.

- A. Næringen er dødt organisk Stof . . . . 16. Klasse. **Saprofyter.**  
 AA. Næring tages fra levende Organismer . . 17. Klasse. **Parasiter.**

Jeg har ved foranstaaende Ordning af Klasserne i første Række taget Hensyn til Ernæringsmaaden samt Mediets og Bundens Natur og Planternes Epharmoni hermed (deres Fasthæftning eller Mangel paa Fasthæftning); og jeg har bestræbt mig for i Literaturen at finde græske Navne, som er betegnende for Klasserne, eller selv at danne nogle, hvis jeg ingen saadanne fandt. Ved dette vanskelige Arbejde har jeg fundet beredvillig Hjælp hos Prof. Dr. A. B. DRACHMANN, for hvilken jeg bringer ham min hjærteligste Tak.

Klasserne inddeles efter andre Hensyn, saasom Arbejdsdelingens Rigdom, Assimilatorernes Former, Livsvarighed o. a., og opføres i følgende Rækkefølge:

1. Hapaxanther.
2. Stedbundne Pollakanther uden særlig formede Organer for Oplagsnæring.
3. Stedbundne Pollakanther med saadanne Organer (Knolde, Løg).
4. Pollakanther med Lysudløbere eller supraterrane Krybskud.
5. Pollakanther med Jordudløbere eller andre Former for subterrane Vandreskud. Herhen ogsaa Rhizomer.

## V.

### 1. Underrække. Vandplanter (Hydatofyter).

Modsætningerne mellem de submerse Planter og Luftplanterne er kortelig angivne S. 127, 134. Vandplanterne er urteagtige, de fleste stedsegrønne og fleraarige. Mellemformer mellem dem findes naturligvis; dog bør Sumpplanterne (Helo-fyterne) henføres til Luftplanterne, fordi deres Assimilatorer for største Delen er til-

passede til Livet i Luften. At Vandplanterne har saa ringe Iltmængde til Raadighed i Sammenligning med Luftplanterne, synes ikke at give sig noget stærkt Udtryk i det Ydre. Dog har det naturligvis Betydning baade for Aandedræt og Assimilation, at Assimilatorerne ofte er delte i mange traadformede Afsnit, og at Intercellulerrummene er saa store.

Vandplanterne kan efter de paa Standpladserne herskende økologiske Faktorer, navnlig Bundens meget forskellige Natur, og den forskellige Tilpasning hertil (Tilhæftningsmaaden) deles i følgende 7 Klasser (se foranstaaende Oversigt S. 134—136).

Foruden de nævnte Forhold er der i Vandet en Mængde andre Faktorer, der har stor Betydning for Arternes topografiske Fordeling, men mindre eller slet ikke for deres Former, saasom navnlig Lysstyrken i forskellig Dybde, Bæltedannelse paa skraanende Bund, Vandets Iltholdighed, Saltholdighed, Bevægelsens Art og Styrke, Varme m. m. En Mængde indifferente Karakterer synes at findes her.

### 1. Klasse. **Smaa-Svæv; Mikro-Plankton.**

Herom henvises her til Literaturen.

### 2. Klasse. **Stor-Svæv; Mega-Plankton.**

Omfatter store, umiddelbart synlige, submers svævende Arter af mange forskellige systematiske Typer. Hertil henføres ikke blot Alger, som *Sargassum*-Arterne, men ogsaa Mosser, saasom submerse Arter af *Riccia*, *Sphagnum* og *Hypnum*, og nogle Blomsterplanter. Nogle af disse har selv Blomsterne under Vand (*Ceratophyllum*), andre hæver Blomsterne over Vandfladen (*Hottonia*, *Aldrovandia*, Arter af *Utricularia* o. a.).

### 3. Klasse. **Flyde-Vegetation (Pleuston).** (C. SCHRÖTER 1896.)

Assimilatorerne har Flydeevne, ligger paa Vandet, i alt Fald i den gunstige Aarstid (flere Blaaagronalger, Arter af Hepaticeer og Hydropteridaler (*Azolla*, *Salvinia* o. a.), af *Lemna*, *Wolffia* o. a. Blomsterplanter, nogle med Rosetskud og Udlobere (*Hydrocharis*, *Stratiotes*, *Pistia*, *Eichhornia*).

### 4. Klasse. **Herpo-Benthos.**

Herhen en Række krybende Blaaagronalger, der ved deres Slimskeder danner løse Overtræk paa Dyndbund, i Sandflader ved Kysterne (»Sandalgelag« i Æstuarierne), i varme Kilder; nogle er utvivlsomt mixotrofe og danner Overgang til Sapro-benthos. Endvidere en Del Bunddiatomeer.

### 5. Klasse. **Rhizo-Benthos.**

Hæfteapparaterne er traadformede, — grenede (»rodliggende«), Rhizoider eller Rødder, der trænger ned mellem den oftest bløde Bunds løse Smaakorn. Nogle

Arter er stedbundne (af Alger i salt Vand *Penicillus*, *Halimeda* o. a., andre har Vandreskud og er samlag-dannende (af Alger f. Eks. *Caulerpa*, Characeer).

Af Kormofyter findes her en stor Del og med forskellig Bygning af Assimilatorerne. De danner Bælter paa Søbundene, og kan opstilles paa følgende Maade:

Helt submerse. Hapaxanthe med Langskudsform: *Najas*, med Rosetskud *Subularia* (maaske ogsaa pollakanth). — Pollakanth med Rosetskud er *Lobelia Dortmanna* og den mixotrofe *Genlisea*, der blomstrer over Vandet. Endvidere med Roset og Knoldstængel: *Aponogeton fenestralis* og *Isoëtes lacustris*. — En Mængde af de helt submerse har Lys- eller Jordudløbere eller Krybskud, Rodstokke eller andre Former af Vandreskud, hvilket formentlig har Aarsagsforbindelse med Livet i Vandet og den lette Dannelse af Rødder i Vand eller i fugtig Bund. Arter af *Helodea*, *Callitriche*, *Myriophyllum*, *Pilularia*, *Potamogeton*, *Zostera*, *Ruppia*, *Zannichellia* o. a. *Helobiales*; nogle faa har Rosetskud (*Vallisneria*, *Littorella*). Nogle har ejendommelige Overvintringsskud (hibernacula).

Andre har Flydeblade med Spalteaabninger paa Oversiden og optager formentlig Kulsyre gennem Luften, saasom den hapaxanthe *Trapa*, en Del Nymphæaceer, Alismaceer, Arter af *Potamogeton*, *Batrachium*, *Polygonum* o. a., der alle er pollakanthe. De fleste har Vandreskud (Udløbere, Rhizoder, Rhizomer) og hæver Blomsterne over Vandet. Tydeligere Overgange til Luftplanterne (Sumpplanterne) findes f. Ex. hos *Hippuris*, *Nelumbo*, *Sparganium*. En saadan Form med Ammeknolde paa Udløbere (»Kartoffeltypen«) er *Sagittaria sagittifolia*.

## 6. Klasse. **Hapto-Benthos.**

Denne Klasse omfatter submerse Planter, der er knyttet til fast Bund, dels haard som Sten, Træ og Bløddyrskaller, dels blødere som levende Planter og Dyr, men som ikke formaar at trænge ind i Underlaget; de er derefter enten Epilither eller Epifyter, og de hæfter sig til Underlaget ved Hapterer (WARMING 1881). Assimilatorerne ligner hverandre deri, at de ikke har luftfyldte Intercellularrum, hvilket formentlig er i Harmoni med, at Arterne vokser i stærkt bevæget, derfor ilt-rigt Vand (fra »Flydebøjerne« hos nogle Alger, som Blæretang og Sargasso, maa ses bort). Iøvrigt er de yderst forskelligt formede.

Epilitherne optræder navnlig i det salte Vand med Hærskarers Mangfoldighed af Algeformer. Formodentlig er disse en urgammel Type, som derfor har formaaet at udforme sig saa mangfoldigt i Harmoni med Standpladsernes store Mangfoldighed i H. t. Lys- og Strømforhold, Bølgeslag, Tidevand m. m. og Bundens Natur og i Harmoni med Lysets Art i de forskellige Dydbælter. Assimilatorerne optræder tillige med tre forskellige Farver.

Til Epilitherne hører endvidere nogle faa Mosser, f. Ex. *Fontinalis*, og Likener (Arter af *Verrucaria*, *Lichina* o. a.; samt dernæst den mærkværdige, mest til tropiske Vandfald knyttede Familie af Blomsterplanter, *Podostemaceæ*, der har mange algelignende Arter.



Epifyter. Til Haptofyterne kan endvidere de epifytiske Vandplanter henregnes, fordi de ved Hapterer fæster sig til andre Planter, særlig store Alger, f. Ex. Laminariaceer, uden dog at trænge ind i dem og tage Næring fra dem. Nogle Arter tager kun Bolig paa bestemte Planter, f. Ex. *Elachista fucicola* kun paa *Fucus*, *Castagnea Zosteræ* kun paa *Zostera*, *Ectocarpus Griffithsianus* paa *Rhodymenia*.

### 7. Klasse. **Endo-Benthos.**

Trænger mere eller mindre langt ind i Substratet, som de vokser paa, og tager Bolig i det uden at være Parasiter i strængere Forstand (d. e. tager Næring fra Substratet; andre synes dog at gøre dette); sædvanlig vokser de der som grenede Traade uden andre Forankrings-Redskaber. Nogle er Endolither, saasom Alger, som formaar at trænge ind i Stene, Bløddyrskaller og andre haarde Legemer (f. Ex. *Gomontia polyrhiza*, *Foreliella perforans* og fl.). Andre Alger er Endofyter, f. Ex. *Stigeoclonium* i *Lemna*, visse *Sphacelariaceæ*, *Streblonema*, *Chælophoraceæ* o. a. imellem Cellerne af andre Alger; utvivlsomt er disse mixotrofe. Andre er Endozoer i Ferskvandsslanger, Skildpadder og Snegle; disse er vel ogsaa mixotrofe.

## VI.

### 2. Underrække. **Luftplanter (Aërofyter).**

Autofyter. Luften eller Luften og Jorden er Livsrummet. De er udsatte for alle fra Luften (Klimaet) stammende Faktorer, og disse faar Betydning for Optagelse, Afgift og Transport af Vand. Det følgende viser, at der er to Hovedformer for Vandoptagelse, nemlig af ærisk Vand og af terrestrisk Vand.

1. Optagelse af ærisk Vand foregaar enten fortrinsvis gennem Assimilatorenes hele Overflade eller gennem begrænsede, særlig til Vandoptagelse tilpassede Dele af Overfladen. Disse Arter er knyttede til en særlig vandfattig, haard og tør Bund, Overfladen af Sten eller af andre Planter og kan maaske kaldes Epifytoïder.

2. Terrestrisk Vand. Hos den anden, langt overvejende Del af Arter sker Vandoptagelsen fra selve Jorden ved Hjælp af Rødder eller Rhizoïder, altsaa grenede, traadlignende Legemer, der trænger ned mellem de mineralske Korn i Jorden og optager Vand og mineralsk Næring ad denne Vej. De kan derfor faa Navnet Chthonofyter (*χθών*, Jord).

En meget væsentlig Afvigelse fra Hydatofyterne er, at Aërofyterne er udsat for Vandafgivelse, hovedsagelig ved Transpiration, i ringere Grad f. Ex. ved Guttation o. a. Dette medfører store, almindelig kendte Tilpasninger af Huden og Legemsformen i det hele.

Endvidere maa Transport af Vand o. a. Stoffer foregaa fra Sted til andet i Plantens Indre gennem særlige Ledningsvæv, i alt Fald hos alle dem, der optager Vandet gennem begrænsede Dele af Legemet.

De epifytoïde Planter maa deles i to Klasser, eftersom de kan optage Vandet gennem Legemernes, altsaa ogsaa Assimilatorernes hele Overflade eller kun paa bestemte, dertil tilpassede Steder. De første har store Ligheder med Vandplanterne og anføres derfor her som første Klasse: *Atmofyter* (*ἄτμος*, Damp). Det angives om mange, at de kan fortætte Luftens Vanddamp til draabeflydende Vand; dette bør maaske staa hen, men i alt Fald kan de optage Luftens Fugtighed som Regn, Taage, Dug, og en dampmættet Luft hører i højere eller ringere Grad til deres Livsbetingelser. De tropiske dampmættede, skyggefulde Skove er især deres Hjem.

Hos de andre Epifytoïder er det ogsaa Regn, Dug og Taage, der er Kilden til Vandforsyningen, men Vandet maa optages gennem bestemt hertil tilpassede Flader eller Dele af Legemerne (Rødder eller haarklædte Strækninger af Assimilatorerne), og Planternes Bygning og Formrigdom bliver derfor langt omstændeligere. Oplagsredskaber for Vand, svarende til Klimaets Periodicitet, findes ogsaa her. Skønt der ingen skarpe Grænser kan drages mellem disse og de epifytoïde, tror jeg dog, at de bør kaldes med et særegt Navn: Regnplanter, Ombrofyter, fordi navnlig Tropernes voldsomme Regnskyl er Kilden til Vand for saa mange af dem.

### 8. Klasse. *Atmofyter*.

Optager draabeflydende, aerisk Vand (Regn, Dug, Taage) gennem Legemets hele Overflade, uafhængig af Rødder og Rhizoïder, om end disse ogsaa benyttes hertil og er mere eller mindre vigtige som Fasthæftnings-Redskaber. De kommer da til paa mange Punkter at ligne Hydatofyterne: Hudvæv mangler eller er mangelfuldt, for Ledningsvævet gælder det samme; ligeledes for det mekaniske Væv. Men de er udsatte for Fordampning. De er Urter, stedsegrønne og næsten alle pollakanthe. Assimilatorernes Former er yderst forskellige efter Arternes systematiske Stilling og andre Forhold.

Som en første Gruppe, den der har størst Lighed med Vandplanter, kan nævnes de, der ikke taaler Udtørring; deres Standpladser er derfor navnlig damprige Tropeskov, Skovkløfter o. a. Standpladser, hvis Luft er  $\pm$  mættet med Vanddamp, og hvis Lys er dæmpet. Hertil hører en Del *Bregner*, navnlig Hymenophyllaceer, endvidere Arter af *Todea* og *Asplenium*. Bemærkes kan, at der er Overgangstyper, som kan taale Udtørring til Lufttørhed, men ikke naaer ny Turgescens alene ved Vandtilførsel gennem Rødderne (f. Ex. *Polypodium vulgare*, *Asplenium Trichomanes* o. a.). Længere varig Udtørring taaler flere Lycopodiaceer (*Selaginella lepidophylla* o. a.). Andre Lycopodiaceer er i høj Grad atmofile.

Andre Grupper af *Atmofyter* er: *Luftalgerne* (Atmofile Alger: J. BOYE PETERSEN), og i Tilslutning til dem endociske Typer af Alger, baade Endolithen (kalkborende), Endofyter (f. Ex. *Chroolepidaceæ* i Blade af Blomsterplanter), Endozoer (f. Ex. *Trichophilus* i Haar af *Bradypus*). Fra dem er der Overgange til snyltende Arter.

*Laverne* (*Lichenes*) maa som en højst mærkelig og stor Gruppe af atmofile Mixotrofer anbringes her. Den almindelige Antagelse er jo, at der er en ejendomme-

lig Symbiose mellem Alger og Svampe. Symbiosen er forskellig hos Arterne. Parasiten tager her Værten ind i sig som sin Slave (Helotisme). Standpladserne er som bekendt meget forskellige (Sten, Træ, Jord) og Legemsformerne ligeledes, hvilket maa tjene til Underafdelinger. FR. ELFVING er Modstander af denne Symbiose-Hypotese. Ogsaa endolithiske Typer findes, for saa vidt som de kan grave sig ind i og grene sig i Kalksten.

**Mosserne.** Assimilatorerne har yderst forskellige Former — orthotrope og plagiotrope, thalløse og kormofytiske. Den anatomiske Bygning er meget enkel; Ledningsstrængene dannes endnu kun af enkle Celler. Vandoptagelse finder vist i ringe Grad Sted gennem Rhizoiderne, men hovedsagelig gennem Assimilatorerne, der har forskellig Tilpassethed til dette Arbejde. Kapillaritet spiller herved en stor Rolle, bl. a. til Opsamling af Vand (Vandsække hos epifytiske Levermosser o. a.).

Laver og Mosser følges ofte ad og danner i Fællesskab store Samfund i forskellige af Jordens Egne, hvor der findes Luftfugtighed og rigelig Nedbør. Mosserne kan som Epifyter danne Tæpper, der i slige Egne driver af Vand. Ogsaa paa Skovbunde, hvor der er dæmpet Lys og tilstrækkelig Fugtighed, dannes Puder og Tæpper, der som Badesvampe kan holde paa det optagne Vand, skønt de hviler løst paa Jorden. I aride Egne er de sjældne. De optræder som Jordmosser, Epifyter, Epilither, Chasmofyter (bebor Klipperevner), Sumpplanter og selv Vandplanter.

*Sphagnum*-Slægternes ejendommelige anatomiske Bygning er beregnet paa Vandoptagelse gennem Legemets hele Overflade, men forøvrigt er Arterne tilpasset til forskellige Standpladser (nogle væsentlig submerse, de fleste andre mere eller mindre terrestre).

Sluttelig kan nævnes en enestaaende, højst mærkelig Type af Blomsterplante, den rodløse Bromeliacé *Tillandsia usneoides*, der optager alt Vand (Dug) og Næring ved Hjælp af sin tætte Klædning af Skjoldhaar, som dækker Skuddenes hele Overflade (se Bromeliaceerne i 9. Klasse).

## 9. Klasse. **Regnplanter; Ombrofyter.**

Under dette Navn sammenfatter jeg Planter, der lever paa fast eller for Rødder og Rhizoïder endog uigennemtrængelig, altsaa yderst tør Bund (Klipper, Træstammer og lign.)

Standpladsen er sklerogeisk. De lever som Epilither og Epifyter i tropiske, regnrige Skove. De kan som Atmofyterne kun optage ærisk Vand, men i Modsætning til disse kun lokalt, gennem bestemt begrænsede Dele af deres Legemer, der særlig er tilpassede hertil. Der maa endvidere være Væv, som overtager det Arbejde at lede Vandet ad bestemte Veje. Nogle Arter formaar at opsamle Muld og danne sig en kunstig Jordbund. De er endvidere nærmest at kalde Haptofyter, fordi de maa holde sig fast til Underlaget ved Rødderne, der har stærk negativ Heliotropisme og Rodhaar, eller ved de krybende Stængler, der ofte ligner og benævnes Rhizomer. Dorsiventralitet kan findes baade hos Stængler og



Rødder. Nogle Klippeplanter fæster sig særlig i snævre Revner i Stenen (Chasmo-fyter, SCHIMPER). Assimilatorerne er meget forskellige efter Arternes systematiske Plads; Arterne er næsten udelukkende fleraarige og stedsegrønne. Ogsaa Rødder fungerer ofte som Assimilatorer.

Vandet optages særlig fra de stærke tropiske Regnskyl. De vandopfangende Redskaber er hos mange Arter Rødderne, der kan være forsynede med Velamen (Araceer, Orkideer), hos andre assimilerende Skud, der kan have ejendommelige, vandoptagende Skjoldhaar (Bromeliaceer). Andre optager Vand paa andre Maader, og tillige findes der hos nogle Indretninger til at oplagre Vandet, baade som Vandvæv og i ydre, ofte kandeformede Hulheder. Rødderne tjener fortrinsvis som Fasthæftningsorganer og har hos mange næsten ingen anden Betydning. Assimilatorerne er sædvanlig udsatte for stærk Fordampning og maa paa forskellig Vis værnes derimod; de bliver da mere eller mindre xeromorfe. Knopperne har ikke Knopskæl. Da Standpladsen selvfølgelig er meget mager paa Næring og Tilgang af Muld yderst vanskelig, findes der hos en Række Typer ejendommelige Indretninger til Opsamling af Muld.

Disse højst mærkværdige Livsformer, som særlig SCHIMPER har studeret, hører til en Række fysiognomisk og systematisk

### meget forskellige Typer,

hovedsagelig følgende:

A. Urter med **Langskud**, oprette og  $\pm$  stedbundne. Vandvæv findes i Bladene, mindre eller slet ikke i Stænglerne.

1. Arter af *Peperomia*, *Begonia* og *Gesneriaceæ*.

2. Nærmest hertil slutter sig en Række epifytiske Orkideer (*Vanda*, *Angraecum*, *Dendrobium*, *Epidendrum*, *Grammatophyllum* o. a.), hvis Skud er mere kortleddede og tætbladede med toradede Blade, dog uden at være Rosetter. Rhizomagtig krybende Grundakser.

3. *Pleurothallis* maa danne en egen Type. Langskuddet bærer en Række Lavblade og ender med et lodret  $\pm$  sukkulent Løvblad.

4. Bladløse, kaktoïde Langskud, trinde (*Rhipsalis*, *Hariota*) eller mere eller mindre bladformede (*Epiphyllum*, *Phyllocactus*).

5. Orkideer med Luftknolde (Pseudobulber), som indeholder slimet Vand og organisk Næring; nogle har enleddede, andre flerleddede Knolde (*Cattleya*, *Lælia*, *Epidendrum*, *Oncidium*, *Coelogyne*, *Maxillaria* o. a.). Rødder med Velamen. Særlig mærkelig er *Bulbophyllum minutissimum*.

B. **Rosetskud** (Helrosetter; egentlige Halvrosetter forekommer næppe); ofte mægtige, stedsegrønne Arter med læderagtige Blade. Mixotrofe er mange, idet Rosetterne opfanger Vand og Planterester, Støv m. m., der danner Muld. Mange Dyr kan leve i dem. Rødderne fæster dem til Underlaget og nogle kan opfange Regnvandet.

1. De enkleste Former med tæt tragtformet samlede Blade findes hos *Araceæ* (*Anthurium*, *Philodendron*), *Liliaceæ* (*Astelia*) og Bregner.

2. **Fuglerede-Typen.** Rosetterne har to Slags Rødder; den ene negativ geotropisk, opadvoksende, danner Fuglerede-lignende Masser, der samler Muld og Vand; den anden hæfter Rosetten til Underlaget. Herhen Bregner, f. Ex. nogle Orkideer (*Grammatophyllum*-Arter) og Araceer.

3. **Nische-Typen:** et stivt, opadrettet Blad af en Roset samler Muld mellem sig og Træets Stamme; de andre Blade er rigere paa Klorofyl, hænger ned og har væsentlig overtaget Assimilationsarbejdet (*Platyserium grande*).

4. **Vandkande- (Cisterne-) Typen.** Rosetbladene læderagtige, rendeformede, slutter forneden tæt sammen til krukkeformede Legemer, i hvilke Vand og Rester af døde Planter og Dyr samles. Næringsoptagelse ved ejendommeligt Hudvæv med Skjoldhaar (Bromeliaceerne). Mest ekstrem er *Tillandsia bulbosa*. De ikke-epifytiske Arter afviger fra de epifytiske.

C. Assimilatorerne er dorsiventrale, thalløse eller mere eller mindre langledede **Krybskud.** Skud af Kormofyter, som ved Hæfterødder bindes til Underlaget. Nogle Arter er »Hemi-Epifyter«, idet de ogsaa sender lange Ernæringsrødder ned i Jorden (Overgang til Klatreplanterne). Skudformerne er væsentlig to Slags.

1. **Nummularia-Typen** har mere eller mindre kredsrunde og kortstilkede, til Underlaget med Randene fasttrykte, hvælvede Blade. Hos nogle ligger Rødderne under Bladene, saaledes værnede mod Udtørring. Arter af *Pothos*, *Philodendron* o. a. Araceer; en Del monopodiale Orkideer, saasom Arter af *Angraecum* og *Aerides*, Asklepiadeen *Conchophyllum*; Bregner, saasom *Polypodium lanceolatum*, Jungermanniaceer (nogle med Vandsække).

2. ***Polypodium vulgare*-Typen**, hvis Løvblade staar mere eller mindre stejlt op fra den krybende Rodstok.

Nogle Arter har begge Skudtyper, f. Ex. *Philodendron* Arter, nemlig *Nummularia*-Typen paa den yngre, sterile Skuddel, men paa den ældre og blomstrende Del Løvblade, der ved lange Stilke føres ud i Lyset.

3. En mærkelig Type er Asklepiadeen *Dischidia*, der foruden Assimilationsblade har krukkeformede Blade, i hvilke der altid er Vand og Rester af døde Dyr, som udnyttes af de ned i Krukkerne voksende Rødder.

D. **Assimilatorerne er Rødder**, stærkt dorsiventrale, hos nogle næsten baandformede (*Teniophyllum*, Arter af *Angraecum*, *Aeranthus* o. a.).

E. **Vedplanter.** Nogle lignose eller sublignose Arter nævnes f. Ex. af Slægterne *Hydrangea*, *Norantea*, *Clusia*; de maa have Muldsamlinger eller Mos paa Træstammerne at vokse i og maa vel regnes til Hemi-Epifyterne. Mærkeligst er Halv-Vedplanterne *Hydnophytum* og *Myrmecodia* med deres af Myrer beboede Knolde.

## VII.

## Jordplanter (Chthonofyter).

Disse er knyttede til den Bund, der er den almindeligste, den porøse og mere eller mindre løse Bund, som dannes af mineralske Korn, mellem hvilke der er Luft, Vand og organiske Smaadele (Sand, Ler, Muld, Morænelag). Fra denne Bund optages Vand og mineralsk samt organisk Næring ved traadformede og grenede Legemer (Rhizoïder og Røddernes Rodhaar). Enkelte Arter formaar at optage ærisk Vand. Røddernes osmotiske Sugekræfter faar stor Betydning for Chthonofyterne.

For Chthonofyterne kommer mange andre Faktorer til at faa Betydning end for Epifytoïderne. Faktorer, som er nøje knyttede til Bundens Natur, saasom Jordens Vandkapacitet, Syredannelse, Gennemluftningsevne, dens Indhold af Mikrober og Dyr og disses Samliv, Næringens Mængde og Art, Mineralsaltenes Art, Vandets Beskaffenhed, Jordbundens Varme osv., i det hele alle de Faktorer, som behandles i en almindelig »Jordbundslære«. Disse Faktorerers forskellige Fordeling i Jorden vil i Almindelighed tilkendegive sig tydelig i Artsfordelingen, foruden i Legemsformerne, hvilket maa danne Grundlag for Chthonofyternes Inddeling i mindst tre Klasser, nemlig Kl. 10, Tørbunds-Saftplanter (Chylofyter), Kl. 11, Saltbundsplanter (Halofyter) og Kl. 12, Sædvanlige Jordplanter (Agrofyter).

Det er først og fremmest Vandøkonomien, der faar sit tydeligste Udtryk i Assimilatorernes Bygning; det er Evnen til at optage Vand i Assimilatorerne og gøre dem saftrige eller kødfulde i Stængler og Blade, der sætter et Skel mellem Klasserne; baade hos Chylofyter og Halofyter kan denne Evne være almindelig og stærkt udviklet: Agrofyternes Assimilatorer er derimod mere eller mindre mesomorfe eller xeromorfe, deres Blade tynde eller læderagtige.

At sætte skarpt Skel mellem de to Klasser Chylofyter og Halofyter alene efter de ydre Former er vanskeligt eller umuligt; en *Salicornia herbacea*, der gennem mange Timer i Døgnet staar i Saltvand til højt op paa Livet, er i sin Assimilators Form ikke væsentlig forskellig fra visse Kaktusslægter, der dog er knyttede til en vandfattig (fysisk tør) og ikke saltholdig Bund, f. Ex. endog er Epifyter. Saftplanternes Blade er i begge Klasser meget enkle i Form; de er oftest smaa, ikke indskaarne og helrandede, uden fremragende Nerver eller Ribber; derimod findes i mange Tilfælde, navnlig hos Tørbunds-Saftplanterne, Torne, der maaske tjener til Værn mod græsædende Dyr. Chylofyterne er næsten alle stedsegrønne.

Ogsaa Stænglerne er saftrige og faar ofte meget usædvanlige Former, navnlig hos Tørbunds-Saftplanterne. Safttrigdommen i Stænglernes og Bladenes Parenkym erstatter Styrkevæv: dette og Forvedning faar her en meget ringere Betydning end ellers: hos ingen andre Livsformer har jeg fundet det saa vanskeligt at skelne mellem Urt og Vedplante som hos Saftplanterne, særlig den tiende Klasse. Perlig-nose Livsformer med Vedringe findes hos nogle, men de mange Arter, som ved Siden af Safttrigdommen har en mere eller mindre forveddet Stamme, bør utvivl-



somt bedst betegnes som sublinnose, navnlig da de ogsaa har andre Ejendommeligheder, f. Ex. Mangel af Vinterknopper med typiske Knopskæl.

Trods de Vanskeligheder, der findes ved at dele Saftplanterne i to Klasser alene efter de ydre Former og Bygningsforhold, tager jeg dog ikke i Betænkning at gøre det, fordi deres Standpladser og formentlig deres dermed i Forbindelse staaende Stofskifte frembyder store Forskelligheder. Den første Klasse, Chylofyterne, er knyttet til en meget vandfattig, fysisk tør Bund og har hjemme i aride Egne med stærk Fordampning; Arterne faar derved i flere Henseender Lighed med den nærmest foregaaende Klasse, Ombrofyterne, og er paa flere Maader knyttet til dem. Den anden Klasse, Halofyterne, er knyttet til en fysiologisk tør, undertiden tillige fysisk tør Bund, nemlig en med Salt imprægneret, ofte meget vandrig eller periodisk oversvømmet Saltbund. Stofskiftet er aabenbart i flere Henseender ejendommeligt og forskelligt i de to Klasser, og om end det endnu ikke er helt forstaaet, bør det dog utvivlsomt bidrage til, at de to Klasser holdes ude fra hinanden (CHERMEZON o. a.).

#### 10. Klasse. **Tørbunds-Saftplanter; Chylofyter.**

Standpladserne er navnlig de mest aride og hede Ørkenegne i Amerika, Afrika, Australien o. a. mindre Omraader. Da Kaarene er saa extreme og tillige saa ensartede, er der udviklet en Epharmoni til dem, der udtaler sig i en høj Grad af Konvergens hos systematisk stærkt forskellige Arter (*Cactaceæ-Euphorbia* og *Stapelia*, *Agave* og *Aloe*, *Crassulaceæ* og *Mesembrianthemum*). Men ogsaa i tempererede Klimater findes de, naar Bunden er vandfattig, lysaaben og Fordampningen stærk (f. Ex. i Klitter).

Hvad der i det nærmest foregaaende er sagt om Saftplanterne i Almindelighed, gælder især denne Klasse.

Fordampningen reguleres hos de fleste især ved Oplagsvandets Slimholdighed, Hudens Tykkelse og Kutinisering, Voks- og Harpikslag o. a., som f. Ex. hos *Sarcocaulon*, ved Spalteaabningernes Nedsænkning, ved Reduktion af Assimilatorernes Overflade (små Blade, Bladløshed), lodret Stilling af Stænglerne og Uddannelse af lodrette Kamme eller Vinger, ved hvilke Assimilationsfladen forøges, men som ikke er saa udsatte for Ørknernes stærke Lysstraaler og dermed følgende Opvarmning. Fordampning foregaar derfor overordentlig langsomt hos Chylofyterne.

Stofskiftet er i alt Fald hos en Række Chylofyter meget ejendommeligt. Arter af *Crassulaceæ*, *Kakteer* og *Mesembrianthemum* ophober om Natten store Mængder af iltrige organiske Syrer, uden at de udskiller Kulsyre; om Dagen afilttes Syrerne da til Kulhydrater, hvormed der bødes paa det ved den anatomiske Bygning vanskeliggjorte Stofskifte.

Mellem høje og lave Typer, mellem Træ- og Buskformer og Dværgtræer og lave Urter er det vanskeligt at drage Skel. Mellem Stængelsukkulenter og Bladsukkulenter (SCHIMPER's Chylokauler og Chylofyller) er det ligeledes umuligt at drage skarpt Skel, fordi baade Stængler og Blade saa ofte samtidig tjener til Vandoplagring.

Assimilatorernes Vækst forgaar gennemgaaende overordentlig langsomt, paa Grund af Assimilatorernes Reduktion og de yderst ugunstige Livskaar.

Chylofyterne optræder med en stor Mangfoldighed af **Typer af Livsformer**. En Oversigt kan gives paa følgende Maade.

### I. Urter; Herbæ.

**A. Hapaxanther.** Urter med alle tre Hovedskudformer, baade Blad- og Stængel-Saftplanter, og med forskellig Længde af Forstærkningstiden. Kortleddede Langskud, ☉ og ☺, har *Sedum annuum*; nærmest *S. villosum*. Langeddede: Arter af *Crassula*. — Nærmest Halv-Roset har Arter af *Mesembrianthemum*. — Pleiocykliske med Roset er Arter af *Sempervivum*, *Anthericum annuum* og navnlig nogle, for deres lange Forstærkningstid berømte Arter af *Agave* og *Fourcroya*; men disses Jordudløbere eller Bulbiller er vel abnormt ikke komne til Udvikling.

**B. Pollakanthe urteagtige Chylofyter** uden Vandreskud. Ogsaa her findes der baade Blad- og Stængel-Saftplanter. Storbladede Langskud har 1) en Del Commelinaceer, Peperomier (der vist alle har Vandvæv paa Bladoversiden), Crassulaceer, *Mesembrianthemum* og *Euphorbia*. 2) Smaabladede Langskud med mere sukkulente, ofte trinde eller halvtrinde Blade. Mange Arter af *Mesembrianthemum*, *Crassula*, *Zygophyllum*, *Sedum* o. a. 3) *Tetraphyle*-Typen. Kortleddede, smaa-bladede Langskud. Arter af *Euphorbia*, *Mesembrianthemum*, *Crassula*. 4) *Anacampseros*-Typen; sukkulent med raklelignende Langskud, der dækkes af pergamentagtige taglagte Akselblade. Nær hertil Apocynaceen *Pachypodium namaquanum*. 5) Bladløse Stængel-Sukkulenter. Salicornioide Saftplanter, hvis Stængler er trinde eller kantede, sukkulente, langeddede med kun smaa eller ingen Blade. Arter af *Ceropegia*, *Sarcostemma*, *Leptadenia*, *Euphorbia*, *Rhipsalis* og *Hariota*; *Stapelia* og beslægtede Asclepiadaceer. Bladløse Stængel-Sukkulenter. 6) *Melocactus*-Typen: Kugleformede, bladløse Stængel-Saftplanter med lodrette Ribber eller Kamme paa Stænglerne. Hertil slutter sig lignende Arter af *Euphorbia*, *Adenium* o. a. 7) *Opuntia*-Typen. Stænglerne byggede op af ofte flade kødfulde Led. *Opuntia*. 8) *Phyllocactus*-Typen. Stænglernes Led bladagtige med en Art Midtnerve. (*Phyllocactus* og *Epiphyllum* er Epifyter). 9) Lignende bladagtige Former hos *Euphorbia*-Arter, men her har de Plads paa en tyk Midterstamme, og hos nogle kastes de af ligesom Blade hos løvfældende Planter.

De her under B. anførte Typer bør utvivlsomt henføres til de urteagtige; de danner nogenlunde en Række, der gaar fra almindelig storbladet Langskudsform til bladløse Stængel-Sukkulenter med Søjle- eller Kugleform. Iøvrigt kan endnu flere Typer indføjes i denne Række.

Pudeform kan fremkomme derved, at Skuddene er korte og har rig Basalgrening.

**C. Pollakanthe Roset-Chylofyter.** Typiske stedsegrønne Rosetter med Bladene rettede til mange Sider er almindelige, sjældnere med kun toradet Ordning af Bladene. Nogle Arter er altid stammeløse og urteagtige, andre, mere forveddede,

faar med Alderen ved Bladenes Afkastning en mere eller mindre høj, nogen Stamme med Rosetterne i Gren-Enderne og faar herved Træ- eller Buskform. Bladene er hos mange meget sukkulente med slimet Cellesaft men uden særlig udpræget Vandvæv, hos andre findes saadant (farveløst, tyndvægget uden Intercellulærer).

Herunder kan en stor Mængde Arter anføres, tildels henførte til forskellige Typer blandt Mono- og Dikotyledonerne.

1. Type: *Sempervivum tectorum*. Kødfulde Urter, hvis Rosetter hviler paa Jorden og ofte er grenede med kort-udløbende Grene, der hver bærer en Roset. De blomstrende Skud dør snart efter Blomstringen. Herhen en Mængde *Crassulaceæ* (*Sempervivum*, *Crassula*, *Echeveria* o. a.), *Saxifragaceæ* (*Saxifraga aizoon*, *S. cotyledon* o. a.), *Aizoaceæ* (*Mesembrianthemum*, næsten udelukkende fra Syd-Afrika; *Galenia*). Endvidere enkelte Arter af *Compositæ* (*Kleinia*) og *Umbelliferæ* (*Eryngium*), samt mange *Liliaceæ* (*Aloe*, *Gasteria*, *Anthericum* o. fl.).

2. Type: *Mesembrianthemum*-Arter med 2 modsatte, hos nogle mere eller mindre sammenvoksede Blade i Skuddene (*M. Bolusii*, *M. bilobum*, *M. truncatellum*). Nogle har lignende Skud, men de er nedgravede i Ørkensandet og har en flad Top med »et Vindue« af Jordbundens Farve, gennem hvilket Lyset kan trænge ned til det paa Legemets Indsider værende Grønvæv (MARLOTH).

3. Type: *Aloe*-Typen. Store eller endog mægtige Rosetter med meget tykke, paa slimet Saft rige Blade. Nogle *Aloe*-Arter har Bladene stillede i 2 Rækker. Arter af *Agave* og *Fourcroya*. Her bør ogsaa mindes om, at der er jordbundne Bromeliaceer. Hos nogle Arter udvikles Stamme.

## II. Sublignoser og Perlignoser.

Medens de under 3 til *Aloetypen* henførte Arter er urteagtige, er der andre Arter af de samme Slægter, der bliver langt mægtigere, busk- eller træformede, med oftest grenet, mere forveddet Stamme og med Tykkelsevækst. I Spidsen af de klodsede Grene bærer de Rosetter af store Løvblade, som periodisk afkastes og paa Stammens Overflade efterlader store, stærkt iøjnefaldende Ar. Herhen af *Compositæ* Arter af *Kleinia*, *Cacalia* og *Senecio*, af *Boraginaceæ* *Echium*, af *Euphorbia* *E. dendroides*, *E. nerifolia*. Hos de store Arter af *Opuntia*, *Cereus* og *Euphorbia* udvikles et Vedlegeme i de ofte træformede eller buskformede Assimilatorers Omkreds, og det synes unaturligt ikke at kalde disse undertiden mægtige Arter for Halv-Vedplanter (Sub-Lignoser), men maaske endog for Perlignoser.

D. Chylofyterne udvikler sjælden særlige **Oplagsorganer** for Vand og organisk Næring eller underjordiske Vandbeholdere. Deres Vandholdighed i Assimilatorerne synes at være fuldt tilstrækkelig for dem, men Exempler paa andre, særlige Oplagsorganer findes. Af Arter med storbladede Langskud kan visse *Sedum*-Arter nævnes (*S. Telephium*-Typen), fra hvis Mellemstokke roeformede Knoldrødder udgaar. I Syd-Afrikas Stepper og Ørkener findes efter MARLOTH Chylofyter med enorme Rødder, f. Ex. Arter af *Euphorbia*; BERGER nævner *Mesembrianthemum*-Arter med Knoldrødder, og i Amerika findes Kakteer med roeformede Vandrødder.



E. Chylofyte Urter med **Vandreskud** findes hos en Del Arter. Af Planter med **Langskud** kan nævnes en Del *Sedum*-Arter, f. Ex. *S. acre*, ligesaa Arter af *Saxifraga*, *Peperomia*, *Mesembrianthemum*, *Zygophyllum* o. s. v. Hos Roset-Chylofyter synes **Vandringsskud** at være endnu almindeligere.

Det nævntes ovenfor, at flere Roset-Chylofyter, hvis Rosetter hviler paa Jorden, har Side-Rosetter paa korte, prostrate eller kort-udløbende Grene (Stolones). Hos nogle Arter frigøres disse Rosetter meget hurtig, saa at de bliver en Slags Yngleknopper (*Sempervivum soboliferum*, *S. stenopetalum* o. a.). Hos andre er Grene længere og mere typiske Lys-Udløbere (f. Ex. *Saxifraga aizoon*, *S. cotyledon*), og hos nogle er de »Flagella«, d. e. Rosetten føres hos disse sidste ud fra Moderplanten paa en lang, tynd og bladløs Stængel, der hurtig forsvinder (Type: *Cotyledon flagellaris*, *Crassula orbicularis*, *Sempervivum arachnoideum* o. a.). Pudeformer og Tæpper, sammensatte af mange smaa Rosetter, fremkommer, naar Sidegrenene er korte og varige (f. Ex. *Saxifraga Elisabethæ*, *S. trifurcata*, Arter af *Sedum* o. a.).

Jordudløbere (Soboles) findes hos nogle (faa?) Roset-Sukkulenter. Mest bekendt er de vel hos *Agave*. En meget afvigende Type er *Sansevieria*; der er kun faa Blade i de paa Enden af typiske, men tykke Jordudløbere stillede Rosetter, og disse Blade har ret forskellig Gennemsnitsform hos Arterne.

#### 11. Klasse. **Saltbundsplanter; Halofyter.**

Halofyterne er knyttet til saltholdig Bund. Deres Standpladser er derfor Bredderne af Verdenshavene og Saltsøer i Indlandene, hvor de har bælteformet Ordning efter Bundens Vandholdighed og Saltholdighed. Endvidere findes de i Ørkener og Stepper med saltholdig Bund. Om deres forskellige Formationer se Økologien.

Det er som nævnt vanskeligt at drage Grænserne mellem dem og Chylofyterne, fordi de allerfleste Halofyter er Saftplanter. Det af Rødderne optagne Salt (Kogsalt, Sulfater, Karbonater o. a.) gør Bunden »fysiologisk tør« og fremkalder Sukkulens. At det er Saltoptagelse, der foraarsager Saltbundsplanters Ejendommeligheder, er paavist ved Dyrkning af Planter paa saltholdig Bund (LESAGE, BATALIN, SCHIMPER, JOHS. SCHMIDT, HOLTERMANN). Men en sikker Forstaaelse af Halofyternes Fysiologi er ikke opnået endnu. Om der end maa skelnes skarpt mellem Chylofyter og Halofyter, har de dog mange Berøringspunkter (CHERMEZON o. a.), og heller ikke deres Standpladser er altid skarpt adskilte. De kan være blandede sammen paa samme Lokaltet, f. Ex. i Klitter eller anden vandfattig og tillige saltholdig Bund.

At Assimilatorerne bliver saftige og kødfulde, skyldes undertiden typiske Vandvæv, hvis Plads kan være periferisk baade i og under Overhuden eller centrisk i cylindriske Assimilatorer, men undertiden en ualmindelig Saftrigdom af Bladenes hele Parenkym. Bladene er ofte saa kødfulde, at de brækker ved Bøjning. At de kan optage saa store Vandmængder, skyldes Cellesaftens osmotiske Tryk. Dorsiventralitet i Bladanatomien findes, men Isolaritet er meget almindelig og vistnok almindeligere end hos Chylofyterne. Særlige Styrkevæv bliver ogsaa her mere over-

flødige paa Grund af Sukkulensen og er derfor sjældne; dog findes lignose Arter, og maaske forholdsvis flere perlignose end hos Chylofyterne.

Endvidere ligner Halofyterne disse i at mangle Overvintringsknopper med Knopskæl.

Assimilatorerne er i Regelen ikke saa rige paa ejendommelige Former som Chylofyternes. Dog findes baade afylle og salikornioide og skælklædte Skud o. a. Gennemgaaende er Bladene smaa, mere eller mindre spateldannede eller linieformede, hele og helrandede og uden større Indskæringer. De fleste Arters Assimilatorer er helt glatte, men stærk og forskelligartet Behaaring forekommer (f. Ex. hos *Tournefortia gnaphalodes*, *Bassia hirsula*, *Atriplex farinosa*, *Obione* o. a.). Torndannelse kan findes, men næppe saa hyppig som hos Chylofyterne.

Den største Forskel mellem de to Klasser synes at være i H. t. Fordampningen; af mine »Halofytstudier« og CHERMEZONS Undersøgelser fremgaar, at Huden hos mange Arter er tynd og lidet kutiniseret, at Spalteaabningerne ligger i Overfladens Niveau og ikke eller kun lidet nedsænkede, at Hypoderm og Forslimning af Hudcellernes Indervægge og andre udpræget xeromorfe Karakterer næsten ikke forekommer. Dette staar formodentlig i Forbindelse med, at Standpladsernes Jordbund i Almindelighed er mere fugtig end hos Chylofyterne, eller endog ligefrem er Vand (f. Ex. for *Salicornia herbacea*), og at Luften ved Havkysterne er fugtig. De Arter, der har det tykkeste Hudvæv, findes især paa periodisk varm og tør Sandbund; stærkest udviklet er det hos Vedplanten *Haloxylon Ammodendron* i Central-Asiens Ørkener. Naar Arter med saadanne Karakterer forekommer, er det vel navnlig paa saltholdig Ørkenbund, som i lange Tider kan være udtørret. Men forøvrigt har fysiologiske Forsøg (af KAMERLING o. a.) vist, at Arter med tilsyneladende udpræget Xeromorfi kan have stærk Fordampning.

Som en særlig Ejendommelighed kan nævnes, at Salt hos nogle udskilles gennem særlige Kirtler paa Assimilatorernes Overflade.

Livsform-Typerne svarer omtrent til Chylofyternes. De kan opstilles saaledes: A. Herbæ. 1. Hapaxanther. 2. Pollakanther med oprette Skud uden særlige Oplagsorganer. 3. Pollakanther med saadanne. 4. Pollakanther med plagiotrope Skud. B. Sublignosæ. C. Perlignosæ.

### I. Herbæ.

1. **Hapaxanther.** — Sommerannuelle med typiske Langskud. Ved vore Kyster findes en Mængde med middelstore, hos nogle mere eller mindre indskaarne, flade Blade (af Slægterne *Chenopodium* og *Atriplex*, *Obione pedunculata*). Med trinde eller halvtrinde Blade og centrisk Vandvæv: *Suaeda*, *Bassia hirsuta*, *Spergularia salina*,

Afylle; *Salicornia herbacea*; centrisk Vandvæv er meget almindeligt i Stænglerne af de afylle Arter.

Efemere Foraarsplanter i afrikanske og asiatiske Ørkener (*Salsola*, *Halocharis*, *Suaeda*, *Halogeton*, *Statice* o. a., se O. PAULSEN o. a.).

Vinterannuelle og Bienne med Rosetskud (*Beta vulgaris*, Arter af *Cochlearia*, *Spergularia*, *Aster Tripolium*). Pleiocykliske Hapaxanther synes meget sjældne.

2. **Pollakanthe** Halofyter er Urter uden Oplagsorganer eller Vandreskud. Det er for manges Vedkommende vanskeligt at faa afgjort, om de er typiske Urter eller sublignose. Langskud, oftest kortleddede og smaabladede med centrisk Bladbygning (*Anabasis*, *Cornulaca*, *Zygophyllum*, *Deverra* o. a.). Rosetskud (eller Halv-Rosetskud) hos mange ved vore Kyster voksende Arter, saasom *Crambe maritima*, *Eryngium maritimum*, *Lepidium latifolium*, *Limonium humile*, *Mertensia maritima*, *Plantago maritima*. Kraftige Pælerødder er her meget almindelige. *Triglochin maritimum* har svag Vandreevne. Pudeplanten *Anabasis aretioides* hører maaske snarest til Sublignoserne.

3. **Pollakanthe** Halofyter med særlige Oplagsorganer synes sjældne.

4. **Pollakanthe** Halofyter, der er sempervirente Kryb-Urter, (*Sesuvium portulacastrum*, *Phloxerus vermiculatus*. — *Ipomæa pescaprae*'s Udløbere kan være baade over- og underjordiske paa tropiske Sandstrandskyster. Herhen ogsaa *Lippia nodiflora*, *Canavalia*, *Batis maritima*, *Salicornia ambigua* o. a.

5. Halofyte Urter med typiske **Jordudløbere** er: *Glaux maritima*, *Halimolobos peltoides*, *Stellaria crassifolia*, *Convolvulus soldanella* (i nogen Grad Slyngplante).

## II. Sublignosæ.

6. Sublignose Halofyter. Buskformede, ofte med grenede Aarsskud. Assimilatorerne har ret forskellig Form og er ofte haarede. Blærehaar danner et tæt Lag paa Assimilatorerne af *Obione portulacoides*, *Atriplex halimus*. Filthaarede, spadedannede Blade har *Tournefortia gnaphalodes*. Linieformede, halvtrinde, glatte Blade, f. Ex. *Suaeda fruticosa*, *Lycium ruthenicum*, *Traganum*.

7. Store, brede Blade, der lig nogle sublignose Chylofyters kastes af og efterlader store, længe varende Ar. Herhen *Scævola Plumieri*.

8. Brede Blade med Kalk secernerende Skæl. *Limoniastrum Guyanum*, *L. monopetalum*.

9. Langskud med smaa, sukkulente, korthaarede Blade. *Salsola vermiculata* o. a. Arter, der har trinde Stængler med salicornioïd Bygning.

10. Langskud med sukkulente Skælblade og ejendommelige, næsten kuglerunde Kortsud. *Halocnemum strobilaceum*.

11. *Tamarix*-Typen. Kortleddede Langskud med Skælblade og epidermale, Salt secernerende Kirtler. Store Buske. Maaske snarest til Chylofyterne.

12. *Salicornia*-Typen. Centrisk Bygning med stort Vandvæv i de leddelte, næsten bladløse Langskud. *Salicornia*; ofte nedliggende Sublignoser med oprette, buskformede Assimilatorer (*S. radicans*, *S. ambigua*). *Arthrocnemum fruticosum*, *Batis maritima*.



### III. Perlignosæ.

13. **Perlignose Halofyter.** Busk- eller træformede. *Haloxylon Ammodendron*. Salicornioide Skud. Træ- eller buskformet. Saltørkener i Centralasien.

14. **Mangrove-Typerne.** Lave Træer i tropiske Kystsumpe med salt eller brakt Vand. Deres mange mærkelige Epharmonier er nu, efter at en Række Forskere har studeret dem, velbekendte (Støtterødder, Aanderødder, Vivipari, Vandvæv i Bladene, Saltudskilning m. m. *Rhizophora*, *Avicennia* o. a.).

15. Maaske kan den i Saltsumpe i Østasien voksende Dværgpalme *Nipa fruticans* ogsaa medtages her.

For Halofyternes Vedkommende er de mange morfologiske og anatomiske Mærkeligheder endnu ikke kausalt helt forstaaede. Endnu mere gælder dette de Oxylofyter, som man har udskilt. Hos mange Moseplanter maa Vandtilførselen af en eller anden Grund hæmmes ved Syrer i Jorden, og Fordampningen gennem Assimilatorerne reguleres derfor i Harmoni hermed (Bladene reduceres, Stænglerne overtager deres Arbejde; Fordampningen nedstemmes ved Vokslag osv.); men Kausalforbindelsen er endnu saa lidet klaret, at det er rigtigst at afvente fremtidige Resultater, før Livsformer opstilles. I mindst lige saa høj Grad gælder dette Nitrofyterne (Ruderatplanter). Afgrænsningen af alle disse Arter fra de til anden almindelig Jord bundne Arter vil iøvrigt være vanskelig.

### Chthonofyternes Klasser.

Under Navn af Agrofytter sammenfatter jeg de Chthonofyter, hvis Standpladser er almindelig porøs og i det hele middelfugtig Bund, og hvis Vandindhold er sædvanligt Ferskvand. Iøvrigt kan Bunden være meget forskellig (Sandjord, Lerjord, kalkholdig, kalkfattig, muldrig eller muldfattig osv.). Assimilatorerne er mesomorfe eller xeromorfe, efter at alle de chylofyller er samlede i de to foregaaende Klasser.

Der maa kunne opstilles i det mindste 3 Klasser, som omfatter en overvældende Mængde af vore sædvanlige Arter, nemlig følgende:

- A. Urter (Herbæ). Afstivning væsentlig ved Turgor.
- B. Assimilatorerne er oftest bredbladede, med fjer- eller haandnervede, tynde, fortrinsvis mesoforme Blade af yderst forskellig Form. Hos nogle, som Liliales, er de ligenervede. 12. Klasse. **Agrofytter.**
- BB. Graminoide Blade, d. e. Bladene er smalle, ligenervede, linie- eller baandformede. Afstivning som i Kl. 12 . . . . . 13. Klasse, **Poioider.**
- AA. Vedplanter (Lignosæ). Foruden ved Turgor finder Afstivning væsentlig Sted ved Tykkelsevækst og Forvedning af Stænglerne og mekaniske Væv . . . . . 14. Klasse. **Xyloider.**

En fjerde Klasse kunde formentlig godt slutes til disse tre, nemlig Klatreplanternes, fordi de aabenbart ganske fortrinsvis har porøs Jord som Standplads lige som Agrofytterne, men aabenbart er sjældne paa anden Bund; men da Assimila-

torerne er saa ejendommelige og paa saa fuldstændig egen Vis er udstyrede til at hæve sig op til Lyset ved Hjælp af andre Planter eller andre Legemer som Støtter, fortjener de at indordnes i en egen Klasse. Desuden er der blandt dem baade Urter, Græsser og Vedplanter. De samles derfor i 15. Klasse. **Klinofyter.**

## 12. Klasse. **Agrofyter.**

Da denne Klasse omfatter saa mange forskellige og tillige karakteristiske Typer, vil det formentlig være hensigtsmæssigt at dele den i et Antal Ordener, navnlig følgende:

1. Orden. **Hapaxantherne.** Urter, der hverken har særlige Redskaber for Oplagsnæring eller Vandreskud. Alle de følgende er Pollakanther.

2. Orden. **Pollakanthe Urter,** hvis Mellemstokke ikke er særlig tykke (crassipede), forveddede eller kødfulde, ej heller har de Vandreskud.

3. Orden. **Crassipede Arter med Xylopodier,** d. e. med brede og tykke, forveddende Mellemstokke, fra hvilke Assimilatorerne undertiden udgaar i stor Mængde, nærmende Planten til Pude- og Tuetyperne.

4. Orden. Arter med **Sarkopodier.** Crassipede Arter med kødfulde, næringsrige Mellemstokke (Knolde, Løg). Assimilatorerne forskellige, ofte enlige og ugrenede.

5. Orden. Pollakanthe Urter med **overjordiske Vandringsskud.** Mellemstokkene sædvanligvis ikke fortykkede.

6. Orden. Pollakanthe Urter med **underjordiske Vandringsskud,** der er tyndstænglede og langeddede. Herunder ogsaa Arter med særlig udpræget Rodskuddannelse.

7. Orden. Pollakanthe Urter med Jordstængler, der baade er tykke, næringsrige og kortleddede, men tillige mere eller mindre vandrette (plagiotrope). **Rodstokke; Rhizomer.**

I disse forskellige Ordener findes dernæst andre Forskelligheder mellem Typerne, saasom i H. t. Assimilatorernes Grundformer, deres Livsvarighed og dermed følgende Epharmoni til Kaarene, Overvintringsknoppernes Bygning m. m. Ogsaa forekommer der Arter, som forener f. Ex. Jordudløbere med Knolddannelse. Disse sjældnere forekommende Typer kan formentlig bedst opføres under de nævnte Ordener.

### 1. Orden. **Hapaxanthe Urter.**

A. **Sommerannuelle (monoeykliske).** ☉. Assimilatorerne er i overvejende Grad Langskud, fordi Udviklingen foregaar uden Afbrydelse gennem en gunstig Periode. Livets Længde er iøvrigt forskellig. De efemere fuldender Livsløbet i faa Uger, i mange Ørkeners korte Regntid. Nogle skal kunne sætte Frugt flere Gange i samme Vækstperiode. Kaarene kan væsentlig forandre Livslængden. Flere smaa Typer kan opstilles efter Skudform, Pladsen for de kraftigste Sideskud, Antydning af Halvrosetdannelse m. m. Exempelvis kan følgende anføres:

1. *Urtica urens*: De kraftigste Grene omtrent paa Skuddets Midte. — 2. *Rhinanthus-Euphrasia*: Halvsnyltare; typiske Langskud. — 3. *Veronica hederifolia*; Lange,

prostrate Skud fra Kimbladakslerne. — 4. *Sonchus oleraceus*: Overgang til Halvroset. — 5. *Geranium molle*: Halvroset mere udpræget. — 6. *Teesdalea nudicaulis*: Typisk Helroset. — 7. *Anagallis arvensis*: Alle Grene prostrate. Undertiden rodslaaende, f. Ex. *Stellaria media*. Normalt stærkt prostrat: *Polygonum aviculare*.

8. *Elatine hydropiper*: Typisk Krybplante. — 9. *Limosella aquatica*: Rosetplante med Flagella.

10. *Raphanus sativus* med knoldformet Primrod plus Hypokotyl. Kulturform.

**B. Vinterannuelle Hapaxanther.** ☉, er dicykliske. Forstærkningsperioden falder i to Aar skilt ved en kold Tid. Rosetskud dannes i første Periode, overvintrer grønt eller halvgrønt med aabne Knopper. Oplagsnæring samles i Regelen ikke. Blomster anlægges undertiden i første Aar. I andet Aar udvikles en blomstrende, enten løvblad bærende Skuddel, f. Ex. hos *Capsella bursa pastoris*, eller et bladløst Skaft (*Draba verna*-Typen). Hos nogle lægger Grenene sig ned i Vintertiden uden at slaa Rod (formentlig Psychroklini), f. Ex. *Vicia angustifolia*. Vinterannuelle findes næppe i Troperne, ej heller hvor Vinteren er særlig kold og lang.

**C. To-aarige (bienne), dicykliske Arter.** ☉☉. Livet er ogsaa her strakt over to Vækstperioder, men det varer længere end hos de vinterannuelle, nemlig 12 Maaneder eller derover. I Harmoni med denne dicykliske Udvikling har Assimilatorerne Halv- (eller Hel)-Rosetform og Oplagsnæring i Hypokotylen plus Primroden, der danner en kraftig, dybt i Jorden nedvoksende Pælerod. I Almindelighed drages Mellemstokken mere eller mindre ned i Jorden ved Rodsammentrækning; Arterne bliver Hemigeofyter. Semivirente med mesofile Rosetblade er vist de fleste. Som Type: *Daucus carota*, til hvilken slutter sig en Mængde Arter i koldttempererede Egne (af *Compositæ*, *Umbelliferae*, *Caryophyllaceæ* osv.). Denne Livsform findes næppe i varme, tropiske Lande, og er vist ogsaa sjælden i de koldttempererede med kort Sommer. Iøvrigt er mange Arters Livsvarighed vaklende (☉, ☉☉, 4) efter Kaarene.

De bienne Arter optræder med forskellige Typer, saasom: 1) *Daucus carota*: Rosetten halvgrøn om Vinteren, Knopperne aabne. — 2. *Pedicularis palustris*: Løvbladene falder af ved Vinterens Begyndelse; Foryngelsesknoppen er dækket af Knopskæl og omslutter Blomsteranlæg. — 3. *Melilotus albus*: Langleddet Langskud; halvgrøn om Vinteren med aabne Knopper. Er formodentlig i sit sydligere Hjem en pollakanth Art, som Klimaet har gjort 2-aarig i Nord-Europa. — 4. *Oenanthe aquatica*: Sumplante med opret, hul, mest langleddet, i hele den nederste, under Vand værende Del ugrenet Stængel. Talrige tynde Rødder fra Nodi. Angives ogsaa ☉ og 4. — De Biennes Standpladser er meget forskellige; de fleste findes paa udyrkede Steder om Byer. Mange er Kulturplanter paa Grund af de mægtige, næringsrige Pælerødder.

**D. Polyenne (pleioecykliske) Hapaxanther.** Assimilatorerne ligner de Biennes, men er ofte langt mægtigere. Mellemstok og Primrod bliver ofte mægtige, kodfulde Oplagsorganer. Som Type: *Angelica silvestris*, til hvilken slutter sig f. Ex. mægtige centralasiatiske Skærmplanter og mange *Compositæ*.



## 2. Orden. *Pollakanthe* Urter.

Stedbundne (Tueplanter) med eller uden særlige Oplagsorganer. Ingen Vandringsskud. Forstærkningstiden før første Blomstring er meget forskellig. Hos nogle bevares Primroden i levende Forbindelse med Assimilatorerne eller Rodstokken, hos andre isoleres deres Skud og selvstændiggøres, idet de forsynes med Birødder. Foryngelsesknopperne er hos nogle aabne, hos andre lukkede ved Knopskæl. Assimilatorerne er, formentlig i Harmoni med Kaarene, mesomorfe eller mere eller mindre xeromorfe. Jordens og Luftens Fugtighedsforhold har stor Betydning for deres Bygning.

Disse pollakanthe, stedbundne Urter uden særlige Oplagsorganer grupperer jeg for Oversigtens Skyld efter Assimilatorernes Former og Forhold til Periodiciteten. Rodsystemets og Mellemstokkenes Former er endnu for lidet kendte.

A. *Sempervirente* Pollakanther. Lysskud oprette, stedsegrønne, ikke redivive. Foryngelsesknopper aabne, uden særlige Dækskæl. Flere Typer.

Langskud. Nogle langeddede, andre kortleddede.

1. *Lycopodium Selago*-Typer. Kortleddede mikrofylle Langskud med undertiden mere eller mindre xeromorfe Blade. Stængelgrunden hos nogle rodslaaende. *Lycopodium*, *Selaginella*.

2. *Commelina*-Typer. Tropiske Skovbunds-Arter med langeddede, storbladede, stedsegrønne Assimilatorer, der udgaar fra Mellemstokke, som ligger lige over eller højt i Jordskorpen. Gaar nær til Ombrofyter og Sarkofyter.

Nogle kan kaldes »Blødstængler«; de har tykke, grønne, svagt grenede Assimilatorer, hvis Løvblade efterlader store Bladar, naar de falder af. Herhen mange Araceer, af hvilke nogle har mange Birødder og kan gaa over til at blive Klatreplanter. *Saxifraga* (*Bergera*) *crassifolia*, Arter af *Oxalis*, *Cissus*, *Curcas*; ogsaa *Gunnera* kan sluttes hertil.

3. *Saxifraga tricuspidata* og andre nivale *Saxifraga*'er. Nogle gaar nær til semivirente Typer, idet Bladene lider meget af Vinterkulden. Assimilatorerne ofte ret stærkt grenede, og idet de er krummede og rodslaaende ved Basis, kan de danne tætte, afrundede Puder og Tæpper. Arter af *Saxifragaceæ*, *Caryophyllaceæ*. Nær hertil en Del Sarkofyler (*Sedum*).

4. *Aphyllanthes monspelienses*. Kort Mellemstok; stive, oprette Assimilatorer, hovedsagelig dannede af 1 Stængelled.

5. Nærmest hertil en Del afylle Umbelliferer fra Australiens (*Trachymene*, *Schoenolæna*) og fra asiatiske og afrikanske Stepper (*Deverra*).

Rosetskud. Sempervirente eller semivirente med Mellemstokke, som ved Rødderne drages ned i Jorden. Findes i stor Mængde i tropiske Højbjærge (jfr. BONNIERS Forsøg), f. Ex. Himalaya, Paramos, Puna. De findes i Slægter, som i vor Natur har helt anden Skudbygning, f. Ex. *Viola*, *Oxalis*, *Senecio*, *Geranium*, *Malva* osv. Mange af disse Arters Mellemstokke er store Xylopodier. Assimilatorerne er paa forskellig Vis tilpassede til at udholde den kolde og tørre Blæst og det stærke Lys. De fleste er vistnok semivirente. Mange Typer.

6. Nærmest herhen i vor Natur f. Ex. *Statice armeria*.

7. *Ananas sativus*. Føres maaske bedst herhen. Stedsegrønne Helrosetskud med linedannede, rendeformede, ved Grunden omskedende, i Randen tornede Læderblade. Andre *Bromeliaceæ* (Se S. 143).

8. *Phormium tenax*. Ridende Blade.

9. Arter af *Eriocaulaceæ* og *Xyridaceæ*.

10. *Tofieldia palustris*; lave Urter med ridende Blade.

11. Bregner med ubegrænset Løvbladrosen paa en skraa eller lodret Grundakse, der dør bort bagtil. Stedsegrøn eller halvgrøn; i nordiske Lande f. Ex. *Aspidium Lonchitis*, *Scolopendrium officinarum*; i Troperne mange andre, nogle med kort, overjordisk Stamme eller endog Træform.

12. Sluttelig synes en Del mixotrofe Arter at kunne føres herhen, saasom de insektivore Slægter *Genlisea*, *Sarracenia* o. a.

#### Halv-Rosetplanter.

Sempervirente. Her synes ikke at findes mange tropiske Arter; Halvrosetskud hører aabenbart fortrinsvis hjemme i tempererede Egne, og sempervirente er utvivlsomt sjældne. Der findes iøvrigt lignende Typer som hos de foregaaende to. Rosetbladene gaar ofte tidlig til Grunde, naar Skuddene strækker sig til Blomstringen, saa at ældre Individuer kommer til at ligne Langskud.

B. **Semivirente** Pollakanther. Assimilatorerne er sædvanligvis mesomorfe og dør aarlig bort undtagen Mellemstokken. Denne bærer Foryngelsesknopperne, hvis ganske unge, endnu udfoldede Blade værnes af de gamle, visne Blades Rester.

Herhen hører en Del Langskudstyper, hvis Stængler undertiden bliver lidt prostrate ved Basis, f. Ex. *Labiatae* (*Nepeta cataria*, *Origanum vulgare* o. a.), *Papilionaceæ* (*Orobis vernus*), *Caryophyllaceæ* (*Spergularia media*), *Compositæ* (*Hieracium umbellatum*), *Polygalaceæ*, *Ranunculaceæ* o. a.

Af Hel-Rosetplanter gives aabenbart en hel Del flere, saasom *Taraxacum vulgare*-Typen og en hel Del andre *Compositæ* med Pælerod; Arter af *Papaver*, *Draba* o. a. *Plantago lanceolata*-Typen afviger bl. a. ved, at Løvskuddene er Monopodier. Nogle *Plantago*-Arter har Pælerod, andre Trævlerodder. *Primula* har endestillet Skaft; *Androsace* o. a. monopodial Bygning. Nogle er sempervirente, andres Foryngelsesknopper dækkes af skællignende Blade. *Sanicula europæa*. Herhen nogle Insektivorer saasom *Drosera*, *Dionæa*, *Cephalotus*, *Land-Utriculariæ* o. a.

Halv-Roset har en Mængde Arter i koldttempererede Lande. De paa mere vandfattig Bund voksende har Pælerod, f. Ex. *Anchusa officinalis*, *Viscaria vulgaris*, *Campanula uniflora*, *Blitum bonus Henricus*, *Cichorium intybus*, *Knautia arvensis*, *Chelidonium majus*, *Onobrychis sativa*, *Potentilla argentea* og mange andre Arter af de samme og af andre Slægter og Familier.

De paa mere fugtig Bund voksende har oftere Trævlerod og bagtil bortdøende Mellemstok. Nogle Arter er efter Kaarene halv- eller helgrønne. Herhen *Ranunculus acer*, *Caltha palustris*, hvis Lovstængler hurtigt isoleres ved Mellem-

stokkens Død: en stor Mængde Arter af *Compositæ*, *Cardamine pratensis*, *Samolus Valerandi* osv.

Monopodiale Typer forekommer ofte, undertiden i Slægter, i hvilke der ogsaa er sympodiale grenede Arter.

C. **Skælklædte Vinterknopper.** Som Overgangsformer til følgende Typer kan nævnes nogle Slægter, hos hvilke det er Løvbladens Foddele eller Tunicæ, der værner de efterfølgende, udfoldede Blade, f. Ex. *Rheum* og *Rumex*.

Rodstokkene af de Arter, der har Knopper med Skælblade, bliver i Regelen trukne ned i Jorden og mere eller mindre skjulte i denne (Hemi- og Hologeofyter). De sædvanlige 3 Former af Assimilatorer forekommer.

Følgende Typer findes:

Langskud.

*Silene venosa*-Typen. Varig Primrod (plus Hypokotyl); grenet Mellemstok. Hologeofyt. Hertil slutter sig mange andre Arter, som dog tildels har Trævlerod, og af mange Familier. Naar en Del er selskabelige paa Grund af underjordisk Vandring, maa bemærkes, at dette her skyldes Rodskud. — Som noget afvigende Type kan *Listera cordata* opfores. Mellemstokken er lodret, tynd og ugrenet, dør bort bagfra.

Helrosetskud.

*Pulsatilla pratensis*-Typen har tyk, dybtgaaende Pælerod. Løvbladens visne Grunddele sammen med Skælblade værner Vinterknopperne. Ofte Hologeofyt, — Afvigende Type er *Hepatica triloba*, idet den kortleddede, monopodiale Grundakse skiftevis bærer semivirente Løvblade og store, tynde Skælblade, der værner Knoppen.

En mærkelig Type kan maaske anføres her, nemlig *Ophioglossum*, der har Mellemstok med 1 Løvblad, og Rodskud.

Halv-Roset-Planter, som mere eller mindre er Hologeofyter.

Varig eller dog længe levende Primrod har Arter af *Pedicularis*, flere Umbelliferer, *Campanula Trachelium*, *Aquilegia vulgaris* o. a. Mellemstok med Trævlerod har *Actæa spicata* og andre Ranunculaceer, *Astrantia major*, *Campanula latifolia*, *Centaurea jacea* o. a. Flere er Hologeofyter, som om Vinteren er helt skjulte i Jorden: de maa da have Oplagsnæring i de underjordiske Stængel- og Roddele. Et Skridt videre i samme Retning gør de Arter, der har særlig formede Oplagsorganer (4. Orden).

D. **Pudeplanternes** Assimilatorer er jo vel oftest kortleddede og overjordiske, smaa-bladede Langskud, der som omtalt er sammentrængte tæt. Det synes, at der ikke findes Knopskæl, men at Assimilatorerne er semivirente. Som Type maa *Silene acaulis* kunne tjene, men iøvrigt er Bladene meget forskellige i Form og Behaaring (hos **DIELS** f. Ex. *Azorella*- og *Aretia*-Typerne). Der er idetmindste to Typer, idet nogle Puder er dannet af et eneste Individ med en dybtgaaende Pælerod eller en xylo-podiumagtig Mellemstok, medens andre er dannet af Skud, der har en rods-laaende



Basis. Pudeplanter findes forøvrigt baade i Polarlande, tropiske Højbjerge og i afrikanske, asiatiske o. a. Ørkener, hvor Forvedningen bliver stærkere (Halvvedplanter, Kuglebuske; se HAURI og SCHRÖTER).

### 3. Orden. **Crassipede Typer med Xylopodier.**

I det foregaaende var der kun Tale om almindelige Mellemstokke, der ikke udmærker sig i nogen særlig Grad ved Tykkelse, ej heller var der Tale om Tilslutning af kødfulde Birødder til Mellemstokke. Jeg vil i dette Afsnit om »tykfodede« Livsformer først nævne de crassipede forveddede, Xylopodierne. Jeg har i 1892 (i »Lagoa Santa«) omtalt og afbildet en Række Mellemstokke, der er særlig tykke og forveddede, mere eller mindre uregelmæssig knoldformede, og som bærer en Tue eller en Gruppe af urteagtige eller halvforveddede, ofte ganske ugrene Assimilatorer. Undertiden lever Primroden længe, men oftest udvikles en Mængde Birødder. Disse Planters Standpladser er den vandfattige Jord i Stepper og Savanner (Campos) i Sydamerika, Sydafrika, Centralasien, Højbjerge i Troperne og andre for Jordbundens Udtørring udsatte Egne. Selv i vor nordiske Natur findes Spor af det samme, som naar Mellemstokken forvedder og bliver stor og uregelmæssig hos en *Artemisia campestris*, en *Poterium officinale* o. a. C. LINDMAN gav dem det udmærkede Navn »Xylopodier«. De er aabenbart Epharmonier med Kaarene, deriblandt Markbrande, idet disse ødelægger de overjordiske Skud, og der derpaa i næste Vaartid rask udvikles mange nye Assimilatorer, som ikke faar Tid nok til at grene sig.

### 4. Orden. **Crassipede Typer med Sarkopodier.**

Andre crassipede Typer er i Modsætning til Xylopodierne kun lidet eller ikke forveddede og har i højere Grad den Opgave at være Organer for Næringsoplag; de er underjordiske, tykke, men kødfulde, bløde og rige paa Vand. Jeg vil derfor kalde dem Sarkopodier. De har en meget forskellig Bygning og morfologisk Natur og har i mange Tider i særlig Grad været Genstand for Omtale i botaniske Lærebøger, selv i Skolebøgerne. De er dog kun extreme Typer af hemi- eller hologeofile Mellemstokke. De kan grupperes saaledes:

A. **Varige Sarkopodier** (d. e. de er perenne, kan leve ofte mange Aar uden tilsyneladende store Forandringer).

B. Overjordiske (Knolde, Løg).

BB. Subterrane (Rødder, Rødder + hypokotyle Stængler, hypokotyle Stængler, epikotyle Stængler).

AA. **Ammeorganer**, d. e. hurtig fortærede Oplagsorganer.

B. Overjordiske (Luftknolde eller Løg eller Knoldrødder).

BB. Underjordiske (Rødder, Knolde, Løg).

Men foreløbig er det vist rettest at lægge den almindelig kendte og tydeligere Inddeling i Knolde (Knoldrødder og Knoldstængler) og Løg til Grund.

## A. Knoldformede Sarkopodier.

### a. Varige Knolde.

1. Luftknolde. Sydafrikas tørre Egne har mange ejendommelige, overjordiske Knolddannelser, hvis Morfologi og Biologi endnu er ret lidet kendt. MARLOTH omtaler dem ofte. Mange, som vokser i den tørre, stenede Karroo, har knoldformede »Rødder« over Jorden, som i mærkværdig Grad ligner Stenene, mellem hvilke de vokser (Mimicry). Som Exempler: et Par Passifloraceer (*Adenia globosa*, *Echinothamnus Pechuelli*), Olacinaceen *Pyrenacantha malvifolia*, Asclepiadaceen *Brachystelma foetidum*, *Euphorbia bupleurifolia*, *Cissus*-Arter (*C. Cruorii* o. a.). Maaske bør disse og andre overjordiske Saftplanter helst henføres til 1. Klasse (Chylofyterne); maaske er nogle snarest kortvarige Ammeorganer.

2. Subterrane Knolde. Mægtige underjordiske Knolde omtales ogsaa fra Sydafrikas Stepper og Ørkener, navnlig af MARLOTH. De maa være tilpassede til disse Egenes ekstremt lange Tørtider. I nogle Tilfælde synes de at være dannede af Hypokotylen alene, i andre af den og Primroden eller maaske ogsaa den nederste Del af Epikotylen. Ligeledes findes mange mægtige Knolde omtalte, delvis afbildede, som forekommende i Højanderne (REICHE, GOEBEL, HAUMAN); heller ikke deres Morfologi og Biologi er tilstrækkelig kendt. De hører til mange forskellige Familier (*Asclepiadaceæ*, *Apocynaceæ*, Pelargonier, *Oxalidaceæ*, *Valerianaceæ* o. a.). Ogsaa Vedplanter kan faa saadanne opsvulmede underjords Organer; MARLOTH omtaler, at i det hele er Rodsystemet meget mægtigt i det karroide Højland.

Af morfologisk bedre kendte Arter med mægtige, varige Rødder kan nævnes f. Ex. *Mandragora vernalis*, *Mirabilis Jalapa* og *longiflora*. Hos *Phyteuma spicatum*-Typen er det først og fremmest Hypokotylen, som grundlægger Knolden. Assimilatorerne er oftest Halvroset.

Knoldene er hovedsagelig en Hypokotyldannelse, der har tynde Birødder, hos nogle Arter med straktleddede Langskud, der er korte og ret kødfulde (Arter af *Tropæolum*, *Gloxinia*, *Claytonia* (nærmest Sarkofyt) o. a. — *Cyclamen*-Typen. Ubegrænsede, hemi- eller hologeofytiske Helrosetskud, dannede af den varige Hypokotyl. Herhen ogsaa *Corydallis cava*, Arter af *Leontice*, *Eranthis hiemalis*. — *Potentilla erecta*-Typens Hypokotyl er den hurtig forveddende Knold med ubegrænsede Roset-skud. Nær hertil *Bunium bulbocastanum*, *Conopodium denudatum*.

*Polygonum viviparum*-Typen har en epikotyl Knold (knoldformet Mellemstok), der er uregelmæssig krummet og bærer Helroset. *P. bistorta*.

En ejendommelig, morfologisk afvigende Type er *Rhodiola rosea*; Mellemstokken er tyk, varig, monopodial og bærer kun Skælblade, fra hvis Aksler udgaar enaarige, ugrenede og løvbladbærende, eventuelt blomstrende Langskud. Herhen ogsaa den meget spinklere *Gentiana pneumonanthe*.

### b. Knolde, som er Ammeorganer.

Disse er kortvarige Oplagsorganer for organisk Næring og Vand, men hvis Opgave det kun er at sætte Udviklingen i Gang efter Hviletiden. Derefter skrumper

de ind og erstattes af nye Ammeorganer for den næste Vækstperiode. Gennemgaaende er Arterne Hologeofyter og redivive, sjældnere Hemigeofyter.

Efter deres morfologiske Natur er Ammeorganerne følgende:

1. Ammerødde. Allerede hos bienne og pluriene Arter findes saadanne, som omtalt S. 153; de udstyres med en nærings- og vandrig, roeformet Pælerod, der fortæres i Løvspringstiden (*Anthriscus silvestris* o. a.). Deres Assimilatorer er forskellige i Form. Langskud har f. Ex. *Dahlia*-Typen, *Sedum Telephium*, *Asparagus Sprengeri* o. a., Helroset *Spiranthes auctumnalis*, Halvroset f. Ex. *Ficaria*. Hertil slutter sig Livsformer som *Ophrys*-Typen og *Aconitum*, *Corydallis solida* og *fabacea* o. a.

2. Knoldstængler, der er Ammeorganer. Mellemstokken bliver en  $\pm$  kuglerund kødfuld Knold, undertiden i Forbindelse med Saftrodder. Arterne er i Regelen hologeofyte, nogle er stedsegrønne og Knoldene  $\pm$  overjordiske, andre er løvfældende. Assimilatorerne har forskellig Form. Af Foryngelsesknopperne har een ofte en bestemt Plads og er kraftigere end de andre (er en »Kraftknop«). Standpladserne er meget forskellige (Stepper, Ørkener og anden lysaaben, vandfattig Bund, men ogsaa Muldbund i Skove (ogsaa tropiske) og Enge, Sumpe osv.).

Herhen hører bl. a.:

a) Jordorkideer med »Luftknolde«, f. Ex. i vor Natur *Malaxis*-Typen, i tropisk Sydamerika Arter af *Cyrtopodium*, *Bletia* o. a. — b) *Ranunculus bulbosus*-Typen. Semivirent Halvrosetskud med endestillet Stand. En flerleddet Del af Stængelens Grund svulmer i Sommerens Løb til Ammeknold, der fornyes næste Aar. — c) *Alisma Plantago*-Typen. Løvfældende, oftest ægformet Knold med begrænset Helroset. Nær hertil f. Ex. *Cicuta virosa*. — d) *Arum maculatum*-Typen. Hologeofyt med sympodial Skudbygning; Ammeknold med Helroset. Hertil en Mængde andre Aracé-Slægter, *Scitamineæ* samt *Crocus vernus*. — e) *Colchicum autumnale*-Typen. Hologeofyt med Efteraarsblomstring. Flerleddet Knold med ejendommelig Morfologi og Udvikling.

I mange andre Familier findes Hologeofyter med Knolde, som endnu kun er lidet kendte, f. Ex. Cucurbitaceer, Ampelidaceer, Urticaceer o. a.; undertiden er de kombinerede med Udløbere eller Ammerødde af Typen »radices filipendulæ«, f. Ex. flere Scitamineer (Arter af *Curcuma*). De omtales senere. Nogle er saa kortvarige, at Arten bliver pseudoannuel,

#### B. Løgplanter (*plantæ bulbosæ*).

Disses Bygning og Biologi er for længe siden bleven udmærket studeret, især af IRMISCH. Mellemstokken (»Løgkagen«) er lodret, yderst kortleddet, bred og forsynet med Trævlerod, der kan drage den ned i Jorden mere eller mindre dybt. Den bærer et større eller mindre Antal paa Oplagsnæring, Vand og Slim rige, derfor kødfulde, skælformede Ammeblade (Løgskæl, Sarkofyller), der slutter tæt sammen, saa at et fast, mere eller mindre kugle- eller ægformet Legeme opstaar. Løgplanterne er i Regelen Hologeofyter, men overjordiske eller hemigeofytiske Arter forekommer ogsaa. Standpladserne har stærkt udpræget Periodicitet.



Assimilatorernes første Løvblade er i Regelen grundstillede (Rosetblade); efter dem følger maaske et nøgent Blomsterskift eller et Langskud. Assimilatorerne bortkastes næsten altid ved den ugunstige Aarstids Begyndelse. Løvbladene er, i Harmoni med deres Kortvarighed, mesomorfe, med tynd, haarløs Hud; dog forekommer ogsaa læderagtige eller noget sukkulente Løvblade.

Løgekagen dør bort bagfra og drages af Rødderne ned i Jorden til passende Dybde (ROYERS »Loi de niveau«). I de hvilende Løg findes ofte Anlæg til Blade og Blomster for den følgende, gunstige Tid. Løgplanterne er derfor for en stor Del Vaarplanter og har »Sommersøvn«.

Til Beskyttelse under Hviletiden findes forskellige Epharmonier, saasom at nogle sydafrikanske Løg af *Oxalis* er forsynede med en stenhaard Skæl eller indhyllede i tykke Trævlelag, som formentlig beskytter dem mod Indtørring. Lignende Epharmonier er utvivlsomt ret almindelige.

Løgplanterne hører for en meget stor Del til Liliaceernes, Amaryllidaceernes og Iridaceernes Familier og træffes derfor især i de Lande, hvor disse har deres største Udbredelse, og som bekendt især i Ørken- og Steppeegne (Sydøst-Europa, Vest-Asien, Sydafrika), men ikke eller meget sparsomt f. Ex. paa Amerikas og Australiens ganske lignende Standpladser.

Foruden i de nævnte Familier findes Løg i enkelte andre, især Oxalidaceerne og Droseraceerne.

Andre Forskelligheder mellem Løgene er, at nogle har sympodial, andre monopodial Skuddannelse; at Ammebladene kan være hele Lavblade eller kun Grunddele af Løvblade; Skudvarigheden er meget forskellig, 1, 2, flere Aar, hvilket formentlig staar i Aarsagsforbindelse med Jordbundens Vandholdighed.

Typer. Som Hovedskillemærke mellem Typerne vælger jeg Forskellen mellem »Bulbi perennes« og »Bulbi annui«. Hos de første opammes Aarets Assimilatorer af Ammeblade, som hører til tidligere Aarsskud; hos de sidste hører alle Ammeblade til samme Akse som den fungerende Assimilator. Ved Frugtsætningen gaar hos disse hele den gamle Plante til Grunde og som Ammeblade for næste Aars Assimilatorer tjener Sideskud paa den; Planterne er pseudoannuelle.

Bulbi perennes med sympodial Grening. Især Liliaceer. *Hyacinthus orientalis*-Typen. Ammebladene lever 2—3 eller flere Aar. Herhen ogsaa *Ornithogalum*, *Lilium*, *Fritillaria*, *Agapanthus*, *Scilla* o. fl.

Bulbi perennes med monopodial Grening. Mindst 2 Aarsskud holder sig friske. Mange Amaryllidaceer, saasom: *Galanthus nivalis*-Typen, *Leucojum vernum*, *Narcissus pseudonarcissus*, *Amaryllis* o. a. Monokotyledoner. Herhen nogle Dikotyledoner: Arter af *Oxalis*, af hvilke nogle har tykke Safttrødder.

Bulbi annui. Hvert Skud lever i to Kalenderaar, idet der i det første anlægges et Ammeløg, medens de ældre Skuddele dør helt bort; i det andet opammes Assimilatorerne, som derefter dør, og et nyt Skud anlægges. *Tulipa silvestris*-Typen, med Arter af *Allium*, *Gagea*, *Iris*, *Tigridia* o. a. Af Dikotyledoner: *Saxifraga granulata*, *Epilobium montanum* o. fl.

### 5. Orden. **Pollakanthe Urter med supraterrane Vandreskud.**

Vandreskuddenes biologiske Betydning er, som anført S. 132, Erobring af ny Jord for Arten, altsaa Opgaver, som fører ud over den enkelte Arts Ernæringsarbejde og Boplads, men som ganske vist har stor Betydning for Forstaaelsen af Samfundenes Sammensætning. Alle Arter med Vandreskud er pollakanthe, og de hører i Form af Assimilator og Tilpasning til Standplads til en eller anden af de allerede anførte pollakanthe Typer; de kunde have været nævnt i Tilslutning til de forskellige stavnsbundne pollakanthe Typer, men Oversigten over deres Former og Biologi vil formentlig blive tydeligere ved, at de alle, som nu, samles i een Oversigt.

Vandreskuddene er allerede kort omtalte S. 132 og 152. Naar jeg her vender tilbage til dem, er det for at pege paa den Betydning, som de har for de af pollakanthe Urters Samfund, og fordi her optræder helt nye Livsformer, saasom Kryb-Urter. Jeg ordner Vandreskuddene paa følgende Maade:

- A. Supraterrane Vandreskud, der altsaa tillige er assimilerende. 1. Prostrate Skud. 2. Buekrummede, rodslaaende Basis. 3. Lysudløbere (Stolones) af forskellige Typer. 4. Kryb-Urter.
- B. Subterrane Vandreskud (se følg. Orden S. 163). 1. Jordudløbere (Soboles). 2. Arter med Rhizoder. 3. Jordudløbere med Ammeorganer. 4. Rhizomer. — Her bør ogsaa Rodskuddene eller de knopdannende Rødder nævnes.

#### **Supraterrane Vandreskud.**

1. Prostrate Skud. Et første Skridt hen mod Udløberdannelsen gør de prostrate Skud, d. e. lange, nedliggende, men ikke rodslaaende assimilerende Skud. Ved vore Kyster og paa varm Klitsand-Bund findes mange Urter med saadanne, hvis Retning aabenbart induceres af Sandets Varme og Lyset, og som kan vise Psychoklini (VÖCHTING, LIDFORSS, TURESON). Efter TURESON kan Skuddene rejse sig igen, naar de ydre Paavirkninger ophører. Fra visse Højbjerge har man iagttaget de samme psychokliniske Fænomener.

2. Buekrummede Skud. Hos mange Tueplanter kan iagttages, at de yderste Skud i Tuen, som, maaske af Pladsforhold, nødes til at lægge deres Grund noget ned og derved berøre Jorden, men snart under Buekrumning søge mere eller mindre lodret i Vejret, paa det buekrummede Stykke af Stængelen slaar Rødder. Særlig er dette Tilfældet, hvor Bunden er fugtig eller vandrig (f. Ex. hos Arter af *Cerastium* o. a. Caryophyllaceer, Arter af *Gnaphalium*, *Polygonum*, *Myosotis* osv.). Ogsaa dette synes fremkaldt af Kaarene. Nogle Arter taber snart Primroden, medens de saaledes isolerede Skud selvstændiggøres. Her kan nævnes Arter med Langskud som *Galium palustre*, og med Halvrosetskud som *Ranunculus flammula*.

En anden Betydning faar denne Skuddannelse derved, at den kan fremkalde **tætte Puder** eller **Tæpper** hos visse Tueplanter, naar de buekrummede Stykker er korte, i alt Fald hos mange Eu-Sarkofyter og Halofyter og Poiofyter, men aabenbart ogsaa hos de nu omtalte Agropyter.

3. Lysudløbere (*Stolones*). Mange Urters oprette Assimilatorer udsender normalt vandrette og rodslaaende Skud fra de oprette Skuds nederste Dele. Disse »Udløbere« kan være meget lange. De træffes utvivlsomt især i middelvarme Lande paa muldrig, ofte fugtig og skygget Skovbund, er mere eller mindre dorsiventrale, mesomorfe, semper- eller semivirente med aabne Vinterknopper. De findes knyttede til de forskellige Assimilator-Typer.

Langskud-Arter med Lysudløbere er f. Ex. *Lamium galeobdolon* og andre Labiater, *Stellaria nemorum*, *Chrysosplenium oppositifolium*; Helrosetplanter med endestillede Stande, f. Ex. *Hieracium pilosella*-Typen med smaa Løvblade paa Udløberne; herhen Arter af *Antennaria* osv. Ubegrænsede Rosetter med begrænsede Blomsterskud har *Potentilla anserina*-Typen; dens Udløbere er traadformede, grenede Sympodier. Omtrent samme Bygning har *Pol. procumbens*, *reptans* o. fl. Begrænsede har derimod *Fragaria*. Halv-Roset har *Ajuga reptans*-Typen; Arter af *Epilobium*, *Valeriana*, *Lychnis* o. a. Lysudløbere med »flagella«, d. e. Udløbere med kun et eneste langt og tyndt, ofte buekrummet Stængelled, der i Spidsen bærer en rig Roset. *Saxifraga flagellaris*-Typen; Arter af *Androsace*, *Ranunculus*, *Elisma*, *Echinodorus* o. a.

4. Kryb-Urter (*Herbæ repentēs*). Herhen regner jeg Arter, som ikke har Udløbere fra en opret, event. blomsterbærende Assimilator, men alene nedliggende og rodslaaende Skud, der bagtil efterhaanden dør bort, medens de fortil vokser videre og grener sig. Herhen:

A. Ubegrænsede Krybskud. a) *Polypodium nummularifolium*-Typen. Ubegrænsede Grundakser med fertile Løvblade. b) *Lycopodium annotinum*-Typen med kortleddede, smaabladede og krybende Langskud, samt lignende oprette, der er fruktificerende. c) *Trifolium repens*-Typen, *T. fragiferum*; en ubegrænset Helroset med Pælerod, der tilsidst dør bort, og langleddede Udløbere med axillære Blomster. d) *Hydrocotyle*-Typen. Ubegrænsede Grundakser med akselstillede Blomsterstande. Med Ændringer i Bladform m. m.; endvidere e) *Lysimachia nummularia*-Typen, hvis møntformede, kortstilkede Blade er stærkt vendt mod Oversiden. »*Jungermannia*-Formen« møder os her paany.

B. Begrænsede Krybskud, semivirente. Som en første Begyndelse til denne Type kan henvises til de S. 161 omtalte *Galium*-Arter. Videre er denne Livsform ført f. Ex. hos *Cardamine amara*-Typen. Krybskuddene bøjer sig opad, begrænses af Blomsterdannelsen, og fra de nedre Dele af det opadbøjede Skud udgaar nye langleddede Udløbere, som senere ogsaa afsluttes af Blomsterdannelsen. Om Vinteren er Udløberne for største Delen raadnede bort, og der er intet andet grønt end Vinterknoppernes yngste Blade (den er semivirent), Hertil slutter sig mange Arter af *Batrachium*, *Veronica*, *Cerastium* (f. Ex. *trigynum*), *Oxalis corniculata*, *Epilobium* o. a. og en Fortsættelse og videre Udvikling findes hos *Zostera* o. fl. submerse Arter (se S. 138). Samme Slægt kan have baade sympodiale og monopodiale Typer, f. Ex. *Veronica*.

C. Vinterknopper med Knopskæl. Meget afvigende er *Asarum europæum*-



Typen. Dens af en Blomst begrænsede Krybskud bærer, foruden 2—3 stedsegrønne Løvblade, 3—4 Lavblade, der som Knopskæl værner Vinterknopperne. — Ret nær hertil gaar Vand- og Sumpplanterne *Calla palustris* og *Mengyanthes trifoliata*. Blomsterstandene er endestillede. Om Vinteren er de bladløse, Knopperne værnede af Bladfødderne eller Bladrester.

Mere eller mindre nøje til denne Type slutter sig følgende med begrænsede Løvblad-Grundakser: *Dichondra repens*, *Linaria cymbalaria*, *Veronica beccabunga*, *V. chamædrys*, *V. officinalis* o. a., *Isnardia palustris*, *Mitchella repens*, Arter af *Pilea* og *Epilobium*. *Callitriche verna* o. a. Noget afvigende er *Viola palustris*, idet Krybstænglerne er mere eller mindre underjordiske og bærer baade Lav- og Løvblade.

#### 6. Orden. Subterrane tyndleddede Vandreskud.

Idet jeg nu gaar over til de subterrane Vandreskud, vil jeg først minde om, at mangfoldige Arter har en udmærket Indretning til Vandring ved deres Evne til at danne Rodskud; man erindre f. Ex. *Cirsium arvense*, *Linaria vulgaris*, *Epilobium angustifolium*, *Rumex acetosella* osv. Alle Slags Assimilatorer er her repræsenterede, og medens nogle Rodskud er »reparative«, for at bruge WITTROCKS Udtryk, kun opstaar som Følge af Beskadigelse, er andre »additionelle«, d. e. de dannes spontant, uden at ydre Vold støder til. Af disse er der atter nogle faa, hvis Rodskud er »necessære«, d. e. at de i større eller mindre Grad er en Livsbetingelse for Arten; til disse sidste hører f. Ex. *Listera cordata*, *Pirola uniflora*, *Ophioglossum*, nogle *Podostemaceæ*, og Halvsaprofyter som *Monotropa* eller Parasiter som *Balanophoraceæ* og *Rafflesiaceæ*.

De egentlige subterrane Vandreskud optræder iøvrigt under følgende Hovedtyper (jfr. S. 152, 161), der er ordnede efter Maaden, paa hvilken de tre ovenfor omtalte Opgaver er løste.

- A. Løvblad-Vandreskud bærer alene eller dog for en Del Løvblade.
  - B. Alene Løvblade = **Bladstauder**.
  - BB. Baade Løvblade og Lavblade.
- AA. Jordstænglernes Blade er Lavblade.
  - B. Jordstænglerne tynde, langleddede.
  - BB. Jordstænglerne tykke, oftest kortleddede..... **Rodstokke (Rhizomer)**.
  - C. Ingen Ammeorganer.
  - CC. Jordstænglerne tynde, langleddede og med Ammeorganer.
    - D. Grene dannes ikke fra nogen bestemt Bladaksel ..... **Jordudløbere (Soboles)**.
    - DD. En Hovedknop fra lovbestemt Bladaksel. **Rhizoder**.

#### Subterrane Løvblad-Vandreskud (»Bladstauder«).

Hermed mener jeg Skud, der plagiotropt vandrer under Jorden, men hvis Blade alene eller for en Del er Løvblade. De maa derfor som Regel alle ligge højt

i Jorden, lige under Overfladen, saa at Løvbladene let kan gennembryde den dækkende Jord. Mange Individuers Stængler kommer dog undertiden eller delvis op til Lyset: Arterne har i saa Fald baade overjords og underjords Skud.

I. Alene med Løvblade. Herhen en Del Bregner, f. Ex. Arter af *Polypodium*, af hvilken Slægt der ogsaa er epifytiske Arter (se S. 143). Mange andre Slægter af Bregner slutter sig hertil, nogle langeddede, andre kortleddede, nogle tyndstænglede, andre saa tykstænglede, at de bør benævnes Rodstokke (Rhizomer). *Pteridium aquilinum*-Typen; mærkelig ved, at Stængelen kan ligge dybt i Jorden, fordi Løvbladene er saa kraftige, at de ved deres Spidsevækst kan gennembryde et endog tykt Jordlag.

II. Grundaksen bærer baade Lav- og Løvblade. *Oxalis acetosella*-Typen. Grundaksen vokser ubegrænset, højt liggende næsten som hos Overfladeplanter. Har baade kødfulde Lavblade paa kortleddede Stængeldele, og langstilkede Løvblade, hvis Basaldele bliver længe staaende, idet de ligner Lavbladene. — *Adoxa moschatellina*-Typen afviger fra foregaaende især ved at være pseudoannuel. — Disse Arter danner nogen Overgang til de ægte Rhizomer.

Hos de følgende er Grundaksen tykkere, kortere og næringsrigere. *Acorus calamus*-Typen. Løvbladrhizom uden Lavblade, med endestillet Blomsterstand, — *Iris pseudacorus*-Typen; den tykke Stængel bærer skiftevis Lav- og Løvblade. — *Butomus umbellatus*-Typen. Monopodial Grundakse; den pløjer sig frem gennem Sumpenes Mudder. — *Nuphar*-Typen, afviger fra den væsentlig ved Bladformen. — *Aspidistra lurida*. Læderagtige Grundblade.

III. Vandreskuddene bærer, i alt Fald efter første Blomstring, kun Lavblade, men har særegne, oprette Assimilatorer. Nogle er tynde og langeddede (Soboles, Rhizoder), andre kortleddede og tykke (Rhizomata). Assimilatorerne hører til de sædvanlige Skud-Typer.

1. Vandreskuddene er tynde og kortleddede; de bærer Assimilatorer med samme Skudform. *Lycopodium alpinum*-Typen. Alle Akser bærer Skælblade.

2. Vandreskuddene tynde og ret langeddede Udløbere. Før første Blomstring bærer de tillige Løvblade; efter denne storbladede Langskud. Ingen særlige Oplagsorganer. — Herhen kan formentlig de følgende henføres: Med Langskud: Arter af *Equisetum*, *Mentha* og andre Labiater, *Mercurialis perennis*, *Circæa lutetiana*, *Stellaria nemorum*, *Asperula odorata* o. a., der er Hologeofyter med Langskud. — Halvrosetplanter er *Aegopodium*, *Achillea*, *Tanacetum* o. a. Compositæ, Arter af *Valeriana*, *Campanula*, *Sparganium* o. a.; de fleste er Hologeofyter. — Helroset har *Tussilago farfara*, *Petasites*, *Convallaria majalis* o. a., der er løvfældende, Arter af *Pirola*, der er stedsegrønne. Til de sidste hører ogsaa en Del Jord-Bromeliaceer, hvis Blade er tyndere, f. Ex. *Lamprococcus chlorocarpus*, flere Bregner, *Gentiana acaulis*, og i Højbjærgene findes en Mængde sobolifere Arter med Halv- eller Helroset-Assimilatorer, hvis Biologi dog er ret ufuldstændig kendt (WEDDELL, HAUMAN o. a.).

3. Arter med Rhizoder, som iøvrigt ligner disse sobolifere Arter, er f. Ex.

følgende. Allerede under Vandplanterne omtaltes bl. a. *Potamogeton*. Af Luftplanter hører herhen f. Ex. *Paris quadrifolia*-Typen (monopodial, 3-leddet Grundakse), nogle Orkideer med sympodiale Grundakser efter første Blomstring (*Cephalanthera*, *Epipactis*, *Cypripedium calceolus*, *Listera*), der alle er Hologeofyter med Langskud.

4. Grundakserne nærmer sig mere til Rhizomer derved, at de er mere kortleddede og næringsrige. Her kan først nævnes *Dentaria bulbifera*-Typen; Hologeofyt med tæt stillede og noget kødfulde Lavblade.

5. *Psilotum triquetrum*-Typen. Rodløse Rhizomer med Mykorrhiza, der fungerer som Rødder. Assimilatorerne er mikrofylle, gaffelgrenede Langskud.

6. *Anemone nemorosa*-Typen. Kortleddet, sympodiale Rhizom med Lavblade og Løvblad plus et endestillet Blomsterskud. *Epimedium alpinum*.

IV. Jordudløbere med særlige Oplagsorganer, der ved dem føres bort fra Moderplanten, som ofte er pseudoannuel. Efter Oplagsorganernes Art fremkommer følgende Typer:

1. Oplagsorganerne er Ammerødder. *Herminium monorchis*-Typen er en Art af Ophrystypen, forsynet med korte Udløbere. — *Lathyrus tuberosus*-Typen. Fra Mellemstokken udgaar der Udløbere med Ammeknold ved Bladfæsterne. — Mange Ammerødder, som hos *Ficaria* (S. 159), plus traadformede Udløbere, har en Del pseudoannuelle *Ranunculus*-Arter. saasom *R. monspeliacus* o. a., *Oenanthe fistulosa*, *Campanula rapunculoides*.

2. Knoldstængler paa Jordudløbere: Pseudoannuelle Arter med Langskud er: *Solanum tuberosum*-Typen; hertil *Stachys paluster* o. a. Labiater, *Oxalis stricta*, *Circea intermedia* og *alpina*, *Trientalis europæa*, *Helianthus tuberosus* o. a. Herhen maa vel ogsaa de *Equisetum*-Arter kunne sættes, der har smaa Stængelknolde, som let løsnes fra Udløberne. Ogsaa nogle faa Hel- og Halvrosetplanter (*Sagittaria sagittifolia*, Sumpplante; *Maranta arundinacea*).

3. *Crepis bulbosa*-Typen. Krybplante, over- eller lidt underjordisk med traadtynde Udløbere, som ender i en Knold.

4. Løg paa Jordudløbere findes hos *Tulipa silvestris*, *Erythronium americanum*, *Triglochin palustre*, *Epilobium palustre*, *Saxifraga granulata* og en Del Gesneraceer (raklelignende). Til disse sidste nærmer sig ogsaa den S. 164 omtalte *Adoxa*.

Ammeorganer synes sjælden at bæres af Rhizoder. Arterne med udprægede Ammeorganer hører næsten alle hjemme paa muldrig, mere eller mindre fugtig og skyggerig Skovjord.

#### 7. Orden. Rodstokke; Rhizomer.

Skønt der ikke kan trækkes nogen skarp Grænse mellem de tyndstænglede (Jordudløbere og Rhizoder) paa den ene Side og de næringsrige Vandreskud (Rhizomer) paa den anden, vil jeg dog samle de sidstnævnte saa vidt muligt for sig her tilsidst. Det drejer sig altsaa om de Rhizomer, der kun bærer Lavblade, men fra hvilke der udgaar Assimilatorer, som i nogle Tilfælde er Langskud, i andre Rosetskud. En Mængde tropiske Arter, særlig af *Scitamineæ*, hører herhen, men er endnu biologisk lidet kendte.



### A. Rhizomer med Langskud.

#### a. Aarlig udvikles kun 1 Skudsæt.

1. *Polygonatum multiflorum*-Typen. Det tykke Rhizom er skælklædt, sympodiale med langeddede, mesofile Assimilatorer og Hovedknop i nogenlunde talbestemt Bladakse. I første Forstærkningsperiode er det Løvblad-Rhizom. Hologeofyt. — *Dichorisandra ovata* nærmest hertil; har »radices filipendulæ«.

2. *Scrophularia nodosa*-Typen. Tykt, uregelmæssigt, ofte knoldformet Rhizom uden regelmæssig Grening. Hologeofyt. Langskud. — *Symphylum officinale*-Typen. Lignende uregelmæssigt Rhizom med halvrossetformet Assimilator, semivirent.

3. *Canna*-Typen. Rhizom, ofte mere eller mindre knoldformet. Ingen Knoldrødder. Langskud med endestillet Blomsterstand. — Nærmest hertil en Del andre Scitamineer (Arter af *Costus*, *Renalmia*, *Alpinia*, *Hedychium*).

4. *Zingiber officinale*-Typen. Rhizomet har korte, knoldformede, mere eller mindre lodrette Led stillede i en enkelt Række. Lysskuddene er to Slags, nemlig dels sterile, ugrejede Assimilatorer, dels Blomsterstande med Højblade. Arter af *Zingiber*, *Amomum*.

#### b. Mange Skudsæt aarlig i sykkelformet Ordning.

*Asparagus officinalis*-Typen.

### B. Rhizomer med Musa-Skud.

5. *Musa*-Typen. *Musa* har stedsegrønne Skud, der udgaar fra et lille Rhizom og nærmest er Rosetskud, hvis Bladskeder er rullede tæt og fast om hverandre til en »Skin-Stængel«. Endestillet Blomsterstand, der tilsidst baner sig Vej gennem »Stængelen«. Skruestillede Blade har Arter af *Musa*, toradede *Heliconia* og *Strelitzia*.

6. *Curcuma longa*-Typen. Knoldleddet Rhizom. Fra de kortleddede Knolde udvikler sig nye Knolde, som søger lodret ned i Jorden. Assimilatorerne er Musaformede Skud, men forøvrigt har *Curcuma*-Slægten flere Varianter, som jeg af Mangel paa Selvsyn maa lade uomtalt. Herhen ogsaa Arter af *Kämpferia*.<sup>1)</sup>

## 13. Klasse. Græslignende Typer (Poioïder).

S. 151 omtaltes, at de autonome Agrophyter, skønt de stiller omtrent de samme Livs krav, formentlig bør deles i tre Klasser, hvoraf de to i det hele er urteagtige, nemlig den første med sædvanligvis bredbladede Assimilatorer og den anden med græslignende Assimilatorer udstyrede (den graminoid). De tilhører Familierne *Gramineæ*, *Juncaceæ*, *Cyperaceæ*, *Restionaceæ* og *Xyridaceæ*. De allerfleste er lave Urter, sjælden over et Par Meter, som især vokser paa lyaaben Bund (Stepper, Savanner, Enge, Græsmarker osv.), hvis Artsammensætning er forskellig efter Bundens Vandholdighed og andre Faktorer; saaledes er de nordamerikanske Præriers Græssamfund forskellige efter den Dybde, til hvilken Rødderne maa gaa ned for at hente Vand. Det synes naturligt og almindeligt at skille disse to store Grupper af Arter fra hinanden — allerede i Genesis gøres jo Forskel paa »Græs« og »Urter«. Jeg stiller

<sup>1)</sup> 12. Klasse fortsættes i 14. Klasse (Vedplanter).

dem her ved Siden af hinanden som to helt parallelle Linier; den ene er ingenlunde overordnet over den anden.

Poioïderne (efter GAMS kaldes de *ποιώδη* hos THEOPHRAST) udmærker sig som velbekendt ved lange, smalle, oftest baandformede, ligenervede Bladplader, Bladroset, lange Bladskeder og visse anatomiske Ejendommeligheder. Det er ikke Stedet at fremdrage disse her. Assimilatorerne hører til noget forskellige Typer; den almindeligste er Halvrosetformen, idet de fleste og længste Blade er tæt samlede ved Skuddenes Grund, hvorfra ogsaa Grenene udgaar. Mellemstokkens Plads er lige i eller over Jordskorpen. Den øvre, straktleddede Skuddel er næsten altid ugrenet nedenfor Blomsterstanden, der hos de fleste begrænser Skuddene; Monopodier kan dog findes, endog i samme Slægt som Sympodier, f. Ex. hos Arter af *Carex* (*C. digitata*, *ornithopoda*, *strigosa*). Helrosetskud findes hos nogle og Langskud hos dem, jeg i det følgende kalder *Arundo*-Typen.

Epharmonien med Standpladsens Natur afspejler sig i Løvbladernes Anatomi. Mesomorfe Blade findes især hos Skov- og Enggræs; xeromorfe hos Klit-, Lynghede- og Steppegræs. Nogle Ørkengræs har stive og stikkende Blade (f. Ex. *Spinifex*). (Halofile Poioïder se WARMING: Halofytstudier.)

De fleste Arter er semivirente; nogle sempervirente (i Troperne er der dog formentlig mange af disse); faa er helt løvfældende, f. Ex. i vor Natur *Phragmites*, *Scirpus lacustris*, *Arundo donax*.

Ogsaa i Røddernes Bygning afspejler sig Epharmoni med Standpladsen. Neddragning af Mellemstokkene i Jorden ved Rødders Hjælp synes meget sjælden, hvilket utvivlsomt staar i Forbindelse med, at saa mange er semper- eller semivirente.

Livsformerne kan opstilles i Lighed med de andre Klassers.

I. **Hapaxanther** findes i alle indenlandske Familier, hos *Gramineæ* f. Ex. i Slægterne *Agrostis*, *Aiopsis*, *Alopecurus*, *Bromus*, *Poa* o. a.; blandt *Cyperaceæ* hos Arter af *Cyperus* og *Scirpus*; blandt *Juncaceæ* Arter af *Juncus*. Foruden dyrkede Arter er det især Tørbunds-Arter, der er Hapaxanther. Af Langskudsplanter kan her nævnes *Zea Mays*, Arter af *Andropogon*, *Oryza* og *Sorghum*. Hapaxantherne er mest sommer- og vinterannuelle.

## II. Pollakanther.

A. Cæspitøse med Halvroset. Tueform uden Udløbere og særlige Oplagsorganer er vel den hyppigste Form; den har meget forskellig Mægtighed og Tæthed fra ganske lave, faa cm høje Arter til »Tussock«-Former, der er 1—2 m høje, f. Ex. *Poa cæspitosa*, *Danthonia*. Tuernes Fysiognomi er forskellig, særlig er der to Hovedformer:

1. Tuer med mere uregelmæssig Grening og alsidig Udvikling, den almindeligste i alle tre Familier optrædende Form, og

2. Tuer, som nærmest har Svikkelform, idet Skuddene staar i en Zigzaglinie, fordi der er sympodial Grening med Kraftknop i talbestemt Bladaksel. Denne Tueform er sjældnere; findes bl. a. hos *Nardus stricta*, *Koeleria glauca*.

3. Helrosetskud har Arter af *Luzula*, *Juncus squarrosus*, *Schoenus ferrugineus*, *Gynerium argenteum*.

B. Rørgræsserne (*Arundo*-Typen) har mangleddede Langskud, der ved Grunden begynder med Lavblade. De synes næsten alle at have Jordudløbere og samles derfor i en følgende Gruppe.

C. *Rhynchospora alba*-Typen har Langskud med kødfulde Lavblade ved Grunden, nærmest Løgskæl. Naar en blomstrende Plante dør, dør Skuddene helt eller omtrent helt, og de grundstillede smaa Løg frigøres. Planten er saaledes pseudo-annuel eller nærmer sig dog hertil.

D. »Bladløse« Skud. En ganske særlig Form af Assimilator er det »bladløse« Skud, der kun — i alt Fald som ældre — bestaar af et eneste langt, endog indtil 3 m langt, grønt Stængelled. Ved Grunden bærer dette dog nogle Lavblade og i Spidsen Blomsterstandene. Denne Skudform, forsynet i Regelen med Rhizom eller Rhizode, findes hos *Scirpus lacustris*-Typen. Endvidere hos *Cyperus papyrus*, andre Arter af *Scirpus*, *Heleocharis*, *Juncus*. Det er Sumpplanter, hvis Mellemstokke og Vandreskud ligger paa Bunden af Vandet; Nyttens af de ejendommelige Assimilatorer synes at være den, at de bedst passer til Bølgeskvulp og stærk Strøm. De maa antages at nedstamme fra løvbladbærende Skud, hvis Løvblade normalt er undertrykte, men undertiden kommer til Syne ved Grunden af det lange Led. Man kan i Virkeligheden ogsaa opstille en Del Arter i en Række, der begynder med nogenlunde typiske Helroset- eller Langskud, fortsætter med faabladede Løvskud (f. Ex. *Eriophorum gracile*), derefter med Løvblade, der er tæt samlede ved Basis, og af hvilke de øverste endnu har smaa Plader (f. Ex. *Eriophorum alpinum*), og ender med »bladløse« Løvskud (f. Ex. *Scirpus pauciflorus*).

E. Stedbundne Poioïder med Ammeorganer. *Rhynchospora alba* synes at være ret enestaaende ved sin Løgdannelse. Det almindeligste er, at særlige Organer for Næringsoplæg er knoldformede (f. Ex. hos *Poa bulbosa*, *Phleum pratense* var. *nodosa* o. a. — *Molinia coerulea*). Selv naar de Arter føjes hertil, hvis Oplægsorganer er knyttede til Udløbere, bliver Tallet af Arter med Ammeorganer dog kun ringe, hvad vistnok staar i Forbindelse med, at Poioïderne i saa ringe Grad er Geofyter og redive.

F. Poioïder med overjords Vandreskud. 1. Den første Begyndelse til Lysudløbere findes hos de mange Arter med ved Grunden bukrummede Skud i Omkredsen af tætte Tuer. Hos nogle bliver de ved Basis paa Grund af Skyggen eller Dækning af Bladrester eller Jord blege Lavbladskud. — 2. Typiske Lysudløbere har en Del Arter, f. Ex. *Glyceria maritima*, *Festuca rubra*, *Agrostis alba stolonifera* o. a. — 3. Typiske Krybgræsser. *Catabrosa aquatica*.

G. Tallet af Arter med Jordudløbere er i Modsætning hertil meget stort, hvilket vel maa sættes i Aarsagsforbindelse med, at Jorden er meget løs (f. Ex. Klitter) eller meget blød og vaad (f. Ex. Strandsand, Dynd ved Søbredder og Kyster). Deres Former er den sædvanlige: Skuddene trinde, Bladene Lavblade, Enderne sylspidse, Birødder ved Bladfæstene. De forekommer almindelig i alle tre store Fami-



lier (f. Ex. *Agropyrum repens*, *Holcus mollis*, *Elymus*, *Psamma*, *Phragmites*), mange Arter af *Carex*, *Eriophorum*, *Scirpus*, *Juncus*.

H. Rhizoder og svikkelformet grenede Rhizomer. Poioïder med Rhizoder, Kraftknop og svikkelformet Grening synes ikke at forekomme hos Gramineæ, derimod findes de blandt Cyperaceerne f. Ex. hos *Carex arenaria*, *Scirpus rufus* o. fl.

Særlig interessante er de Arter, der har Rhizoder forenede med bladløse Assimilatorer og svikkelformet Grening af de mange Skudsæt, som aarlig udvikles. De er fortrinsvis Sumpplanter. Foran (S. 168) omtaltes *Scirpus lacustris*. Herhen ogsaa *Heleocharis palustris*, *H. uniglumis*, nogle Arter af *Juncus*.

Hos nogle er Grundakserne Rhizoder, d. e. de er langeddede, hos andre er de Rhizomer, d. e. kortleddede, men med samme svikkelformede Grening. Begge Former kan findes hos samme Art, f. Ex. *Juncus balticus*. Det er Kaarene, der giver det forskellige Fysiognomi, idet nemlig Jordbundens løsere eller fastere Bygning og større eller mindre Vandrigdom er det afgørende. Det samme er afgørende for, hvormeget de tueformede Arter faar Pudeform; denne optræder især hos Arter, der vokser under slette Kaar, f. Eks. i Ørkener og Højbjærge (i Australien efter DIELS, Sydafrika efter MARLOTH, Andesbjergene efter HAUMAN og TSCHUDI; se endvidere HAURI og C. SCHRÖTER).

I. Jordudløbere forbundne med Oplagsorganer. Varige Knolde anlægger *Scirpus maritimus* ved Grunden af Assimilatorerne.

Andre Knolddannelser har *Scirpus parvulus*, *Cyperus esculentus* og *Juncus nodosus*.

K. Nogle meget ejendommelige Typer af Poioïder er de afrikanske Arter *Priodium palmato* og *Schoenodendron Buchneri*, der nærmer sig til at være Sublignoser.

Sluttelig kan ogsaa som Sublignoser Bambuseerne nævnes. De er eller nærmer sig i alt Fald til de plurienne Hapaxanther derved, at naar de efter mange Aars Vegetation blomstrer, gaar de eller store Mængder af dem ud (mon helt?) — i Brasilien som i Indien.

Medens Bambuseerne ved deres Jordstængler danner tætte Buskadser i Skovbryn og paa Skovjord i Troperne i det hele, og medens mange andre Poioïder er knyttede til Sumpe, og her ved Hjælp af deres vandrende Jordstængler danner endog mægtige Samlag (*Phragmiteta*, *Scirpeta*, *Papyreta* osv.), er de allerfleste andre Typer knyttede til muldrige Græsmarker og Enge og til Lavmoser, hvor de optræder dels stedbundne, dels med Jordudløbere; mange xerofile Træplanter er knyttede til tørre Stepper, saaledes er f. Ex., efter WILLKOMM, »milevide Arealer« i Nordafrika dækkede af de xerofile Esparto-Græs (*Lygeum*, *Macrochloa*).

#### 14. Klasse. Vedplanter (Xyloïder; Plantæ lignosæ).

Turgor og Styrkevæv er de vigtigste Midler, ved hvilke Luftplanternes Dele antager og bevarer Form og Stilling; Turgor fortrinsvis hos de urteagtige, Styrkevæv fortrinsvis hos Vedplanterne; Tykkelsevækst hjælper med for de sidstes Vedkommende. Vedplanterne er, paa meget faa Undtagelser nær, pollakanthe. Mellem Urter og Vedplanter er der en vældig Forskel, selv om der, selvfølgelig, er de utal-

ligste Mellemformer. Vedplanterne kan navnlig føje Skud til Skud og hæve sig højt over Jorden i en mægtig, overjordisk Bygning, der kan trodse maaske Aarhundreders ublide Kaar. Ved deres Størrelse har Vedplanterne en væsentlig Fordel under Kampen med de lave Urter, som vokser i deres Skygge.

Forvedning afhænger i væsentlig Grad af Kaarene; visse Omraader af Jorden (KÖPPENS »Dendrochorer«) er i særlig Grad rigere paa Vedplanter, navnlig Træer, i Forhold til deres Urteflora. Der er for længe siden gjort opmærksom paa, at Slægter, som i koldttempererede Egne er rige paa Urter eller alene repræsenteres af Urter, allerede i Vinterregnsomraaderne er rige paa forveddede Arter; jo mere man, f. Ex. i Frankrig, nærmer sig Middelhavslandene, desto almindeligere bliver Forvedning. Paa Madeira og De kanariske Øer er mange Slægter, der i Nordeuropa kun repræsenteres af Urter, rige paa forveddende Arter (f. Ex. *Brassica*, *Echium*, *Chrysanthemum*, *Hypericum*, *Sonchus*, *Solanum*, *Viola*, *Plantago*, *Geranium* o. fl., jvfr. M. VAHL). I Troperne findes Familier repræsenterede af Træer, der i tempererede Lande kun tæller Urter eller lave Sublignoser (f. Ex. *Liliaceæ*, *Labiataæ*, *Solanaceæ*, *Polygonaceæ*).

Sublignoser og Perlignoser. Forvedningen er langtfra lige omfattende hos alle Lignoser; hos nogle (Halv-Vedplanterne, Sublignoserne) bliver de øverste Skuddele mere urteagtige end de nedre og dør bort ved Slutningen af Vegetationsperioden, idet der over Jorden bliver en Slags Stub (Mellemstok) tilbage, der dog kan være saa høj, at den omfatter den allerstørste Del af Aarsskuddene. I Modsætning til dem kan de stærkere forveddede, hvis hele vegetative Aarsskud lever videre til næste Aar, kaldes Perlignosæ (Hel-Vedplanter). Disses Højder og Levealder er derfor som Regel langt større end Sublignosernes, og andre Forskelligheder findes ogsaa, der især er knyttede til Knoptyperne.

### Fysiognomiske Typer. Skudformerne.

Begreberne »Træ« og »Busk« bør være rent fysiognomiske og intet have at gøre med Udstrækningen af Skuddenes Forvedning; Træet (*δένδρον*) har een, opret, højere eller lavere, indtil en vis Højde grenløs Stamme, der er søjlefast og bærer en af de fungerende Assimilatorer dannet Roset- eller Grenkrone. Rosetkronen er oftest ugrenet, dannet alene af rosetstillede, mægtige Blade, oftest faa i Antal; Grenkronen er dannet af en oftest stor Mængde af grenede Løvskud (Langskud) med mange Blade. Jo større Antallet af Blade er, desto mindre er de i Regelen. Busken har ingen enkelt ved Højde eller Tykkelse udmærket Stamme; et større eller mindre Antal omtrent lige kraftige Løvskud udgaar lige ved Jordfladen eller i den allerøverste Jordskorpe, idet de stræber lodret eller skraat opad; den har en »siddende« Krone; en Art Mellemstok kan findes. Mellem Træ og Busk er der nærmest kun kvantitativ Forskel. Ved Trægrænsen i Højbjærgene forkrøbler Vedplanterne, og Træerne synker ned først til Buskform, højere oppe til nedliggende eller krybende Former. (Om de plagiotope Vedtyper se senere.) De danner fysiognomisk forskellige Samfundsformer, Træerne Skov, Buskene Krat, Dværgbuskene Heder (eller Ris-Heder). Trærnes og Buskenes forskellige Typer optræder for-

øvrigt med mange andre Forskelligheder, der ikke blot skyldes Kaarene, men ogsaa genotypiske Forskelligheder (Grenstilling, Grenretning, Grenbygning, Bladformer m. m.), som fremkalder et forskelligt Fysiognomi, der kan gøre Arterne kendelige endog i stor Afstand.

Assimilatorernes Skudformer er de samme som i de foregaaende Klasser, nemlig Rosetskud (meget sjælden Halvrosetskud) og Langskud, hvilke sidste kan være saavel lang- som kortleddede. Desuden findes under disse en Række særlige Former, der nævnes nedenfor som særlige Typer.

Særlig bør bemærkes, at der ved Siden af utvivlsomt ægte, rene Autotrofer findes en Del Mixotrofer, der skaffer sig anden Næring (Kvælstof) som Halvsnylttere (særlig Loranthaceer) eller ved Mykorrhizer, eller anden Symbiose, f. Ex. Bælplanterne og Hvidæl ved kvælstof-samlende Knoldbakterier.

Bladenes Form og anatomiske Bygning er overordentlig forskellig efter Slægtskab og Kaar. Her kan der mindes om, at Vedplanter findes ikke blot blandt Agrofytterne, men ogsaa hos Chylo- og Halofyter samt Klatreplanter.

Periodiciteten. Standpladsernes store Forandringer i Aarets Løb i H. t. Mængden af Fordelingen af Nedbør, Varme og Lys sætter selvfølgelig i paafaldende Grad sit Præg paa Lignosernes stærkt udsatte Assimilatorer. Mange er sempervirente, ikke blot rosetkronede, men ogsaa grenkronede; mange er løvskiftende, faa aabenbart semivirente undtagen blandt Sublignoserne.

Hviletidens Knopper er aabne hos Rosetlignoserne, der jo ogsaa for største Delen er tropiske eller subtropiske, sempervirente Arter. Hos de tropiske, træformede Grenlignoser er de oftest meget smaa og i det højeste værnede af smaa, grønne Skælblade (ufuldkomne Løvblade eller Akselblade), men typiske tørre Knopskæl kan forekomme (se WARMING: Lagoa Santa). Derimod har de koldttemperede Landes Lignoser oftest store Knopper, utvivlsomt fordi Arbejdstiden er saa kort, og at alle Blade samt Blomster derfor maa anlægges Aaret før Udspringet. Dernæst har de gennemgaaende typiske tørre, brune Knopskæl til at værne de spæde Anlæg i det Indre. Der er enkelte træformede, der ingen Knopskæl har og dog kan holde ud i Klimater, der ikke er tropiske eller subtropiske, f. Ex. *Cupressus*, *Thuja*, ja selv vor *Juniperus communis* kan tælles med her. Naar Trævækst ophører i nivale Egne, er det næppe, fordi de i Knopperne indesluttede unge Anlæg ikke er godt nok beskyttede, men fordi de udviklede vegetative Skud dræbes.

**Aarsskuddene.** Rosettræernes Aarsskud grener sig for mange Slægters Vedkommende slet ikke (Træbregner, Palmer, Cykadeer o. a.), og de, der grener sig, danner næppe mere end et Grensæt aarlig. Hos mange Grentræer udenfor Troperne danner de i Vinterregnens Omraader og i Stepperne voksende Arter næppe mere end 1 Skudsæt aarlig; i de koldttempererede Egne er der nogle Arter, hvis Aarsskud grener sig (danner »Sommerskud«), især naar Ernæringskaarene bliver særlig gunstige, men i Tropernes Regnskove er grenede Aarsskud næppe sjældne (MALME o. a.). Sublignoserne staar ogsaa i dette Punkt nærmere Urterne end Perlignoserne.



**Oplagsnæring.** Vedplanterne har ikke en saadan Rigdom paa særegne Oplagsorganer som Urterne. Hos dem oplægges baade Vand og organisk Næring især i Assimilatorernes Stængeldele og Rødder, hos nogle ogsaa i nogen Grad hos de overvintrende Løvblade; men de paagældende Plantedeles ydre Former røber dette kun i sjældne Tilfælde (knoldformede Rødder hos *Spondias tuberosa*, Arter af Proteaceer og Eucalypter o. a. fra aride, ørkenagtige Egne, og en Del Sublignoser saasom *Manihot utilissima*; »tøndeformede« Stammer hos visse Bombaceer, navnlig i særlig hede og tørre Tropeegne (*Chorisia ventricosa*, *Bombax globosum*, *Eriodendron, Cavanillesia*) og andre Familier (*Cucurbitaceæ*, *Euphorbiaceæ*, *Apocynaceæ* o. a.). Det er vel især Vand, der oplægges i disse Stammer, hvis Ved er let og blødt. I Egne med udprægede Kuldeperioder skifter Oplagsnæringens Art efter Aarstiderne, Stivelse forsvinder og genoptræder, Sukker og Fedt dannes (RUSSOW, FISCHER, O. G. PETERSEN, VÖCHTING, LIDFORSS).

Lignosernes Vandoptagelse. Vand og mineralsk Næring optages af Lignoserne hovedsagelig gennem Rødderne, der hos mange gaar meget dybt, hvorfor de er mindre afhængige af overfladiske Vandlag end f. Ex. Urter og Græsser. Naar ældre Træer bliver toptørre og dør, skyldes det vist oftest, at de er blevne for høje til, at Vandet med Lethed kan hæves saa højt. Mellem Kaarene og Rodsystemets Mægtighed er der ofte paafaldende Harmoni; f. Ex. angiver MARLOTH, at i det karroide Højlands aride Egne har Buske med Højde som en Menneskehaand ofte meterlange Rødder, og saadanne Dværge kan vel være 30 Aar gamle. Rødderne har vist yderst sjælden Kontraktionsevne, hvilket aabenbart staar i Forbindelse med, at Assimilatorerne rager saa højt op i Luften og varer saa længe.

Usædvanligt Arbejde overdrages derimod de saakaldte »Støtterødder« (*Rhizophora*, flere Palmer, *Ficus* o. a.) og »Brætrødder« hos mægtige Urskovstræer; endvidere »Aanderødderne« i Sumptræernes luftfattige Mudderbund (*Taxodium*, *Avicennia*, *Brugiera* o. a.). Nogle Rødder omdannes til Torne, formodentlig som Værn mod Angreb af Dyr.

At trække skarpe Skel mellem Herbæ, Sublignosæ og Perlignosæ er umuligt. Jeg vil dog forsøge at pege paa nogle af de Ejendommeligheder, som jeg anser for mest karakteristiske for hver af de to lignose Grupper.

Sublignoserne har 1) hyppigst lav Vækst; 2) kortere Levetid; 3) Busk- og Dværghuskform; 4) mangler typiske, tørre Knopskæl; 5) er ofte semivirente; 6) Aarskuddene er ofte grenede; 7) Grenenderne dør  $\pm$  bort ved Arbejdstidens Slutning; 8) hyppigere Forekomst af Vandreskud, navnlig af Jordudløbere; 9) hyppigere Forekomst af særlige Redskaber for Oplagsnæring.

Baade Sub- og Perlignoser optræder med følgende Former: 1) Oprette, grenede Skud. Herved maa bemærkes, at Rosetplanter naturligst synes at maatte skilles fra Langskudsplanter, og at de til en vis Grad er særlige sublignose Typer. 2) Pude- og Tæppeformer findes hos begge. 3) Lysudløbere findes hos faa. 4) Jordudløbere aabenbart hos endnu færre, særlig de træformede Arter.

### 1. Orden. Roset-Lignoser.

Disse synes saa afvigende fra Gren-Lignoserne, at de fortjener at opstilles for sig, i en særlig Orden.

Roset-Lignoserne er karakteriserede i det foregaaende (oftest sempervirente med aabne Endeknopper, oftest ganske ugrenede eller i det højeste faa grenede Assimilatorer). Ingen særlig tydelig Tykkelsevækst ved et Vækstlag. De store fysiognomiske Forskelligheder, der findes her, synes kun i ringe Grad at være epharmoniske.

#### I. Kryptogamer og Monokotyledoner.

Følgende Typer kan udskilles:

A. Indskaarne eller delte Løvblade. Herhen 3 Hovedtyper. — 1. Bregnetypen. Mange Skovbundsplanter med mesomorfe Løvblade, andre xeromorfe. Træbregner af Slægterne *Alsophila*, *Cyathea*, *Dicksonia*. Bladene ofte stærkt indskaarne. Ejendommelig Vækst. — 2. Cykadétypen. Stammerne uden eller med faa klodsede Grene. Xeromorfe, læderagtige Blade. Sæt af Lavblade skifter med Sæt af Løvblade. *Cycas*, *Dioon*, *Encephalartos*, *Macrozamia*. Standpladser oftest lysaabne, mer eller mindre tørre. — 3. Palmerne. Kun *Hyphæne* grener sig normalt med faa klodsede Grene. To konstitutionelle Typer: Fjerpalmer og Viftepalmer; Xeromorfi. Hapaxanther er nogle faa (Arter af *Corypha*, *Metroxylon*).

B. Udelte, helrandede,  $\pm$  læderagtige Blade; i det højeste Randtorne. — 4. Lilietræernes Typer. Bladene fra bredere Grund jævnt afsmalnede, xeromorfe, læderagtige,  $\pm$  kødfulde (nær til Chylofyternes Klasse: Aloëtypen). *Dracæna*, *Yucca*, *Dasyllirion*, *Vellozia*, *Pandanus*, *Xanthorrhoea* o. a. Af Bromeliaceer f. Ex. *Puya chilensis*. Standpladser mest aabne, vandfattige, solrige Trope- eller Ørkenegne. — 5. *Ravenala*-Typen. Ubegrænset Stamme med vifteformet stillede Blade af Scitaminétypen.

#### II. Roset-Lignoser, der er Dværgtræer.

Af de nævnte Typer findes der mange helt eller næsten helt stammeløse Arter, hvis Kroner med omtrent kugle- eller halvkugleformede Stammer ofte maa siges at hvile paa Jorden. Navnet »Busk« passer ikke paa dem, bedst vistnok »Dværgtræer« (blandt Bregnerne f. Ex. Arter af *Angiopteris* og *Marattia*, blandt Palmerne *Chamærops*, *Geonoma*, mere afvigende *Nipa*; blandt Cykadeerne *Zamia* o. a.; blandt Liliales *Xanthorrhoea*, *Yucca*). Heller ikke vil Navnene »Pudeform«, »Espalierform« o. a. Former passende kunne anvendes paa slige lavstammede typiske Helrosetplanter.

### 2. Orden. Dikotylar og Gymnospermer.

#### A. Helrosetplanter.

Blandt disse findes kun nogle ganske faa, endnu til Dels lidet kendte Typer, der kan kaldes Helrosetplanter, f. Ex. afrikanske Arter af *Lobelia*, *Senecio* og Araliaceen *Cussonia*, samt i de amerikanske Højbjærge Compositeen *Espeletia*. Maaske kan Gnetaceen *Tumboa Bainesii* (*Welwitschia mirabilis*) fra Sydafrikas Ørkener bedst finde Plads her.

Særegne Oplagsorganer synes ikke at forekomme hos de nævnte Roset-Lignoser; dog kan nævnes de knoldformede Stammer, der er store Vandbeholdere, f. Ex. hos *Nolina*, samt at nogle Arter af *Dracæna* og *Sabal* har mærkelige, ned i Jorden voksende Jordstængler.

### B. Dusktræer.

En ejendommelig Type af dikotyle Gren-Lignoser synes at danne en Slags Overgangstype fra de ægte rosetkronede til de mest typiske grenkronede, idet den har Bladene duskformet samlede i Enderne af lange, nøgne, udspærrede Grene, som kun er faa i Tal. Kronerne er derfor meget lysaabne, hvilket formodentlig er i Harmoni med Standpladsernes Lysforhold. Dette synes at være en vidt dreven Form af den Ejendommelighed hos mange Tropetræer, at deres Løvblade er færre, større og fastere, men mindre ensformig fordelte paa Grenene end de extratropiske, navnlig tempererede Landes Træer; dissers Grene er rigere grenede, og deres Løvblade tyndere og talrigere og fordelte mere jævnt over hele Skuddets Længde.

Som Type paa Dusktræ kan nævnes *Cecropia*. Mere eller mindre nøje slutter sig hertil f. Ex. *Terminalia Catappa*, *Carica Papaya*, *Hippomane mancinella*, *Aspidosperma*, Arter af *Rhizophoraceæ* (JOHS. SCHMIDT) og flere andre, saasom formentlig Arter af *Plantago*, *Robinsonia* og *Dendroseris* fra Juan Fernandez Øerne (SKOTTSBERG).

Til Rosettyperne nærmer sig ogsaa en Del Arter, der nærmest maa kaldes Sublignoser, saasom Arter af *Statice* og *Echium*.

### C. Typiske grenkronede Lignoser.

Først hos de grenkronede Lignoser fremtræder Typerne »Træ« og »Busk« samt »Espalierbusk« med hele deres fysiognomiske Præg, og tillige bliver Modsætningen mellem Sublignoser og Perlignoser skarpere, baade fysiognomisk og biologisk. Skudformerne er mange og meget forskellige, og i det hele de samme hos Sublignoser og Perlignoser. Som de vigtigste Skudformer fortjener at nævnes først de utvivlsomt sublignose Typer, dernæst de faa særlig perlignose Typer, som kan føjes til dem.

**Sublignose Typer.** De sublignose Typers Assimilatorer er Langskud, undertiden kortleddede. Nogle er stedsegrønne, andre halvgrønne eller løvfældende. Blad- og Skudformer er meget forskellige. De ordnes saa vidt muligt efter Fordampningsintensiteten.

a. Assimilatorerne har kun 2-aarig Varighed.

1. *Rubus idæus*-Typen (*Virgultæ* KRAUSE). Fra en Mellemstok udvikles oprette Langskud, der kan være grenede; i andet eller et senere Aar udvikles paa dem korte Sidegrene med Løvblade og Blomster. Derefter dør det hele Skudkomplex ned til den korte Mellemstok. Foryngelsesknopperne er skælklædte. (Andre Arter er Halvlianer.)

b. Assimilatorerne varer i det hele længere Tid.

2. *Acanthacé*-Typen. Buskformede Skovplanter, c. 1—3 m høje, stedsegrønne, i det hele glatte eller dog kun spredthaarede, svarende til Skovenes dæm-



pede Lys og fugtige Luft osv. Ofte store, tynde Løvblade, oftest med Indskæringer i Randen. Mange tropiske Skovplanter (*Acanthaceæ*, *Piperaceæ*, *Rubiaceæ*).

3. *Veronica*-Typen. Buskformede, stedsegrønne, med glatte, noget glinsende, helrandede, noget læderagtige Blade. Mange nyzelandske *Veronica*-Arter; herhen maaske ogsaa *Polygala myrtifolia*, en Del til *Caryophyllaceæ* hørende Arter (af *Dianthus*, *Gypsophila* o. a.) med ofte smalle Blade; semper- eller semivirente, idet de øverste Skuddele ikke forvedder.

4. *Myrtus communis*-Typen. Glatte, stedsegrønne Langskud med helrandede, ofte noget læderagtige, kortstilkede Løvblade med indsænkede ætheriske Oliekirtler. Ingen ægte Knopskæl. Hertil kan maaske ogsaa sluttes en Del *Verbenaceæ*, *Rutaceæ*, *Hypericaceæ* o. a.

5. *Euphorbiacé*-Typen. Mælkende. Løvbladene er ofte store, helrandede, glatte. Nogle, maaske de fleste, er løvfældende Buske, andre semivirente (f. Ex. *Euphorbia dendroides*; Arter af *Asclepiadaceæ* o. a.).

6. En Række Arter udmærker sig ved brede, ofte store Blade med en eller anden Form for Behaaring, bl. a. følgende: *Datura arborea*-Typen. De unge Skud blødt filthaarede, hvid- eller gullighaarede, mest eller alene paa Undersiden; ogsaa Stjernehaar eller spindelvævformet Haarklædning kan forekomme. Arter af *Solanum*, *Artemisia*, *Cistus*, *Croton*, *Sparmannia* osv. Nogle har Træform, andre Buskform.

7. *Salvia*-Typen; »det bullate Blad«, med ætheriske Olier i Kirtelhaar. Hos mange buskformede Xerofyter springer Ribberne netformet frem paa Undersiden af de xeromorfe Blade, hos de mest extreme saa stærkt, at der mellem dem dannes ret dybe, haarklædte Fordybninger (Gruber), i hvilke Spalteaabningerne ligger. Ofte bliver Bladet kammerdelt derved, at Bastbelægningen naaer fra Nerverne ud til Huden paa begge Sider. Arter af *Salvia*, *Cistus*, *Lantana* o. a. Slægter; Standpladserne er lysaabne, tørre, varme, især i Vinterregnsomraaderne (Garigues, Macchia, Klitter, Stepper).

8. *Lavandula*-Typen. Oprette, lave, vellugtende Smaabuske af Labiaternes, Verbenaceernes, Cistaceernes o. a. Familier; den staar *Salvia*-Typen nær, men Bladene er lange, smalle,  $\pm$  lancetdannede, og hos mange er Randen rullet noget tilbage, saa at hele Undersiden ofte bliver een, hvid- eller graafiltet Fure. *Lavandula vera*, *Rosmarinus officinalis* osv. Standpladser: Garigues ved Middelhavet, Klitter og Stepper, Vinterregnsomraader osv.

9. *Buxus sempervirens*-Typen. Smaa, stive, læderagtige, glatte og glinsende Blade. Former som Træ, Busk, Pude og Espalier. Stedsegrønne. Nogle perlignose med Knopskæl.

10. *Erica*-Typen. Langskud, kortleddede med tætstillede, korte, liniedannede, læderagtige og stive Blade, der paa Oversiden er glatte og glinsende; paa Undersiden (sjældnere paa Oversiden) er der en dyb Fure, i hvilken Spalteaabningerne ligger. Stedsegrønne. Nogle har Knopskæl, andre ikke. Herhen en Del Slægter af *Ericaceæ*, *Empetrum* o. fl.

Oftest Dværg-Lignoser og Espalierplanter, sjælden lave Træer paa tørre Standpladser.

11. Mikrofylle Typer. Mikrofylle, kortleddede Assimilatorer med skælførmede,  $\pm$  taglagte Blade. Stedsegrønne. Ingen typiske Knopskæl. Grenede Aarsskud. *Cupressus*, *Thuja*, *Juniperus*, *Tamarix*, *Elytropappus* o. a.

12. Pinus-Typen. Lange, liniedannede Skud, omtr. isodiametriske Blade med Spalteaabningerne overfladisk liggende. Herhen mange Arter af *Conifera*, *Asparagus*, *Plantago*, *Myricaria* o. a., nogle med Knopskæl, andre uden.

Assimilatorerne  $\pm$  afylle; Assimilationen besørges væsentlig eller alene af Stænglerne. Stedsegrønne. Træer, Buske.

13. *Spartium*-Typen. Langleddede trinde Langskud; Aarsskuddene ofte grenede, stedsegrønne. Løvbladene smaa, mesomorfe, falder hurtigt af. Spalteaabningerne hos flere i Furer paa Stænglerne. Grenenderne dør bort hos nogle. Nogle har ingen Knopskæl, andre har grønne Skælblade om Knopperne. *Spartium junceum*, *Sarothamnus*, *Genista*, *Retama*, *Deverra* o. a.

14. Fladskud-Typer. Assimilatorerne er langledede, flade eller vingede Akser, efter at Løvbladene er faldne af. Stedsegrønne. *Genista sagittalis*, Arter af *Baccharis*, *Colletia*, *Mühlenbeckia*, *Bossiaea*.

15. *Ephedra*-Typen. Langleddede, trinde, stedsegrønne Assimilatorer. Bladene er reducerede til ubetydelige, totandede Skeder. Spalteaabninger i dybe Furer. Træer, Buske, Halvlianer. *Ephedra*.

Tornskud. Hos mange Vedplanter i arid Natur dannes Torne af forskellig morfologisk Natur. LOTHÉLIER og andre har vist, at deres Fremkomst direkte kan skyldes Standpladsens Tørhed og stærke Lys. Tornkrat i Sydafrika, Garigues, Epinals osv.

16. Løvbladene naaer ingen betydelig Størrelse, falder ofte tidlig af. Buske af forskellig Højde. I Regelen er Tornene vistnok Værn mod Græsædere, men der tales dog ogsaa om »Torntræer«, f. Ex. Akacier i Afrikas Steppegne, hvor der jo ogsaa er mægtige Planteædere. Herhen Arter af *Colletia*, *Berberis*, *Lycium*, *Ulex*, *Genista*, *Hippophaë*s o. a. (*Ruscus aculeatus*).

Lignose Halvparasiter. Mykorrhizer forekommer spredt omkring blandt Typerne, og at samle dem i en egen Gruppe er ikke godt muligt, tilmed da deres biologiske Betydning er uklar. Men en enkelt Type af mixotrofe Livsformer kan dog fremhæves, nemlig den halvsnyltende

17. Loranthacé-Type. Buskformede, stedsegrønne Vedplanter, der selv snylter paa andre Vedplanter. Xeromorfe Typer; de fleste som *Viscum album* med ret store læderagtige Løvblade og Knopper uden Knopskæl; andre med bladløse, vingede Stængler. Nærmere om dem kan her forbigaas.

Sublignoserne findes vel næsten over hele Jorden — som Underskovsplanter i de tropiske Regnskove, i dæmpet Lys i Skovbrynene eller i dybe Kløfter, og her mest mesomorfe. De xeromorfe har derimod Standplads især i lysaabne, aride Egne.

**Perlignose Typer.** Perlignosernes Assimilatorer er til Dels ganske de samme som Sublignosernes. De største Forskelligheder, som kendes allerede saa godt fra vor egen Natur, er den mellem stedsegrønne og løvfældende. De halvgrønne er sjældne. Fremdeles mellem Arter med og uden typiske Knopskæl paa Vinterknopperne; de sidste er sjældnere end hos Sublignoserne. Af Assimilatorer er nogle Typer almindeligere hos Sublignoserne, f. Ex. Filtbladformen, *Lavandula*-Typen, *Erica*-Typen o. a.

Derimod er langeddede Langskud med store, glatte, mesomorfe eller  $\pm$  læderagtige, xeromorfe Løvblade almindeligere hos Perlignoserne; herhen hører f. Ex. vore egne Løvtræer og de allerfleste tropiske Skovtræer. Laurbærbladet, Ficusbladet, Myrtebladet, de sammensatte Blade hos *Leguminosæ* og andre Former; endvidere er Naalebladet almindeligere blandt Perlignoserne (Naaletræerne i det koldtempererede Bælte).

Træformen er almindeligere hos Perlignosæ, og her findes store Forskelligheder i Kronfysiognomien, som har faaet Udtryk i mange Adjektiver (Kronen er kegleformet, pyramideformet, ægformet, skærmformet osv.). Dværgtræer er almindeligere her, og findes navnlig under ugunstige Kaar (Tropernes Savanner, Campos og Stepper; de øverste Træbælter i Bjærgene. Nogle af disse Dværgtræer er Modifikationer, forkrøblede Individer, fremkaldte ved kolde Vinde, kold eller tør Jord og andre ugunstige Kaar; andre synes arvelig faste.

Af Buskformerne er Højbuske, mellemstore Buske og Smaabuske almindeligere blandt Perlignoserne end blandt Sublignoserne. Som Smaabuske er velbekendte *Myrica gale*, Arter af *Rhododendron*, *Vaccinium*, *Cassandra*, *Daphne*.

Dværgbuskene er ofte omtrent halvkugleformede med rig, tæt og uregelmæssig Grening. Undertiden er de nedre Grene nedliggende og rodslaaende, hvorved Overgang dannes til Krybbuske. (Saaledes hos *Calluna*, *Ledum palustre*, *Cassandra calyculata*, *Juniperus sabina* og *nana* o. a.), men Primroden bevares oftest længe hos dem, og Birødderne er sædvanlig haartynde. Hos Dværgbuskene er Karaktererne vist saa blandede, at Adskillelsen i Sub- og Perlignosæ ikke lader sig gennemføre. Dværgbuskene danner Grundlaget for egne Samfundsformer: Heder, Buskstepper. De optræder ogsaa med Pudeform især i Polarlande, Højbjærg og Stepper.

Som foran bemærket findes **Oplagsnæringen** hos Lignoserne i det hele i Stængler og Rødder uden at gøre sig bemærket ved ydre Fremtræden; her bør dog lige bemærkes, at nogle Arter har Knoldrødder, saasom *Manihot utilisima*, og paa lignende Maade forholder sig aabenbart en Del sydafrikanske »Halvbuske«, det vil vel sige Sublignoser, saasom Arter af *Pelargonium*, Skærmlplanten *Anesorrhiza capensis*, og *Elephantorrhiza Burchellii*. Denne sidste, der har mægtige Luftknolde, bør maaske snarere føres til en anden Type.

I Modsætning til denne Form for Variation i Lignosernes Livsformer, spiller Forekomsten af **Vandreskud** en meget stor Rolle.

#### A. Epigeiske Vandreskud.

En Mængde Sublignoser har prostrate Skud. Det er aabenbart, at Kaarene kan fremkalde saadanne; paa Stenrevler paa vore Strande optræder f. Ex. *Prunus*



*spinosa* med fladt udbredte, nedliggende Skud, til hvis Formdannelse maaske baade Bundens Varme, Sollyset og Vindene har bidraget. I den ægyptiske Ørken optræder lignende Former paa stenrige, solaabne Steder (VOLKENS). I Alperne er der f. Ex. *Rhamnus pumila* og *saxatilis*. Rimeligvis kan Roddannelse med paafølgende Aflægning finde Sted hos flere. Her kan erindres om, at perlignose Træer kan have nedliggende og rodslaaende Grene (*Picea excelsa*, *Coccoloba uvifera* o. a.).

Der er kun et lille Skridt videre frem til ægte **Espalierdannelse** med Rodfæstning. Der er Arter, som kan optræde med ægte Træform og Buskform, men ogsaa, formentlig ved Vindpaavirkning, synke ned til lave Espalierformer, f. Ex. *Juniperus communis*. Af andre, der kan synke ned til Espalierform, kan nævnes *Betula nana*.

Andre Arter maa betegnes som konstante Espalierplanter eller Krybplanter, f. Ex. *Empetrum nigrum*, *Salix reticulata* o. a. Arter, *Arctostaphylos*-Arterne, *Cassiope tetragona* o. fl.

Nogle af disse Espalier- og Krybplanter er Sublignoser, andre Perlignoser. Til Sublignoserne bør saaledes *Dryas octopetala* regnes; den er nærmest en flad Træplante med kraftig Pælerod og Birødder fra de nedliggende Skud. Aarsskuddene er grenede, uden Knopskæl. Bladene hører snarest til den bullate Type med hvidhaaret Underflade. *Arctostaphylos uva ursi* er derimod en perlignos, stedsegrøn Krybplante, hvis Primrod lever længe, og hvis nedliggende Skud danner kraftige Birødder. Aarsskuddene er i Regelen ugrenede; Løvbladene xeromorfe, læderagtige; Knopperne har Knopskæl.

**Kryb-Lignoser med Ranker.** d. e. lange, langeddede og tynde Skud, der er lidet grenede og efterhaanden dør bort bagfra. De mest typiske er sempervirente — *Oxyccoccus palustris*-Typen. Aarsskud med Knopskæl og oftest begrænsede. Nærmest til den *Myrtus nummularis*, *Polygala chamæbuxus*. *Linnæa*-Typen. Sublignose uden Knopskæl. Ubegrænsede Langskud, oprette blomstrende Sideakser.

#### B. Hypogeiske Vandreskud.

Her kan først mindes om de skuddannende Rødder, som nævntes S. 133. Mange Træer og Buske har som bekendt saadanne, oftest er det dog de lavere Træer. De høje Skovtræer har det aabenbart sjældnere; særlig rigelig findes de hos *Populus tremula*, *Hippophaës rhamnoides*, flere af vore Frugttræer osv.

Egentlige subterrane Vandreskud forekommer baade hos Roset-Lignoser, f. Ex. visse Palmer (Arter af *Chamædorea*, *Mauritia*, *Rhapis flabelliformis*, *Dracæna*, *Cordyline*, *Kingia australis* o. a. Af Gren-Lignoser kan nævnes en Del Buske, bl. a. *Syringa vulgaris*, *Lonicera Xylosium*, *Symphoricarpus racemosa*, *Philadelphus coronarius*, Arter af *Rosa* og andre middelstore Buske; *Myrica gale*, *Andromeda polifolia*, *Vaccinium myrtillus* og *Vitis idæa* og mange andre Dværglignoser. Som en af de mindste kan *Chimaphila umbellata* nævnes. Bladformer, Skudbygning, Overvintringsmaade og Knophygning er ret forskellige hos disse lave Lignoser, hvad jeg her maa forbigaa.

### 15. Klasse. Klatreplanter (Klinofyter); Lianer.

Klatreplanterne er rodfæstede især i porøs, muldrig Jord, fra hvilken de ved Rødder optager Vand, og knyttede til Standpladser med fugtigt Klima; men mest karakteristisk for dem er, at deres Assimilatorer i Modsætning til de autonome Atmofyters (8. Kl.) ikke formaa at holde sig opret ved egen Kraft, men søger Støtte hos andre Legemer, især andre Planter. De er derfor almindeligst i høje og tætte Plantesamfund (Skov, Krat, Enge o. lign.). Et ret stort Antal Familier har Repræsentanter mellem Klatreplanterne; de optræder meget spredt i Systemet, hvad der tyder paa Nedstamning i forskellige, af hverandre uafhængige Linjer.

Det er naturligt, at man her maa finde forskellige Skudformer, med forskellige biologiske, morfologiske og anatomiske Afvigelser fra de autonome Arters, epharmoniske med Klatremaaderne, hvilket for længe siden har gjort dem til meget yndede Studieobjekter (MOHL, DARWIN, SCHENCK, TREUB, SCHIMPER o. a.). I samme Plantesamfund kan meget forskellige Typer optræde, hvilket antyder, at Skudformerne ogsaa er genotypisk faste.

Klatreplanterne er baade Vedplanter og Urter, hapaxanthe og pollakanthe, løvskiftende og stedsegrønne Arter. Det epharmoniske i Bygningen er især følgende:

Karakteristisk for Assimilatorerne er, at de alle er straktledede Langskud, tynde og ofte meget lidet grenede, indtil de er naaet op til stærkere Lys i Støtternes Toppe. Rosetskud forekommer næppe. Skuddenes Stængeldele iler i Udvikling ofte langt forud for deres Blade, hvorved opnaas, at Skuddene ikke bliver saa tunge mod Spidsen og lettere kan skyde sig ind mellem Støtteplanternes Grene. DARWIN skelner mellem følgende 4 Hovedtyper af Klatreplanter: 1) Slyngplanter, 2) Arter med pirrelige Gribeorganer, 3) Arter som klatrer ved Hæfterødder, 4) Arter som klatrer ved Hager eller Kroge. Hos SCHENCK og andre findes de samme Grundformer.

Bladformerne er hos flere Typer meget karakteristiske; hos Slyngplanterne og Rodklatrerne meget ofte langstilkede, med fra Stænglerne udspærrede Stilke og brede, hjerte- eller nyreformede Plader (f. Ex. *Convolvulus*, *Hedera* o. a.). Pladen staar sædvanlig omtrent vinkelret paa Stilken og faar formentlig derved de bedste Belysningsforhold. Løvbladene er vel oftest mesomorfe, men andre Typer forekommer, selv sarkomorfe, og nogle Arter er nærmest bladløse.

Stænglerne er jo meget ofte stærkt udsatte for Snoninger og Bøjninger. Den Fare for Ødelæggelse, som de herved er udsatte for, modarbejdes ved højst usædvanlige anatomiske Bygningsforhold, som fyldig er omtalte og afbildede i Literaturen. Især kendes saadanne fra *Bignoniaceæ*, *Menispermaceæ*, *Dilleniaceæ*, *Sapindaceæ*, *Leguminosæ*, *Piperaceæ* o. fl. De beslægtede, men ikke klatrende Arter i de samme Familier afviger derimod ikke fra de sædvanlige Bygningsforhold. En Ejendommelighed er dog mere udbredt og fælles, nemlig at de stoffledende, anatomiske Elementer, Vedkarrene og Sirørene, er usædvanlig vide og lange, et nyttigt Bygningsforhold for saa lange og tynde Stængler. En stor Mængde Lianer udmærker sig

iøvrigt ogsaa ved Vandrigdom. Hugges i Troperne et Stykke af en større Lian, kan man ofte se Mængder af Vand strømme ud.

Blandt Klatreplanterne finder jeg i alt Fald følgende Typer.

### 1. Orden. **Halvlianer** (SCHENCKS »Spreizklimmer«).

Saaledes benævnedes jeg 1892 (»Lagoa Santa«) de »sarmentøse« Lianer, som synes at staa de sædvanlige autonome Planter nærmest i Bygning. Det er Arter, hvis Klatreevne kun bestaar i, at de kommer til Vejrs ved at stikke deres lange, tynde, ofte bukrummede Skud ind imellem andre, højere Planter og lade dem hvile paa disse samt holde sig fast mellem dem ved udspærrede, smaa Grene, Blade eller oftere ved Torne eller tilbagekrummede Kroge; men disse Legemer er ikke pirrelige. Halvlianerne har især hjemme i Skovbryn, Hegn og Krat, mellem Højstauder og i andre lavere Samfund. Herhen flere Typer.

1. *Rosa*- og *Rubus*-Arter; *Galium aparine*; Arter af *Scleria*.

2. Brachiata Arter. d. e. med armformet udspærrede Grene, der hviler paa Støtterne (*Chiococca*, *Lycium*, *Bougainvillea*, *Buddleia*, *Peireskia*, *Bambusa*).

3. Arter med »flagella« (*Calamus*, *Desmonchus*, Rotangpalmer).

### 2. Orden. **Slyngplanter** (*Plantæ volubiles*).

Uden at være pirrelige ved Berøring lægger Stænglerne sig i højre eller oftere venstre Skrue om en lodret Støtte. Herhen en Mængde Arter, baade Urter og Vedplanter (*Humulus*, *Convolvulus* osv.).

### 3. Orden. **Rodklatrere**.

Stængelen er negativ heliotropisk og lægger sig derfor tæt op til Støtten, til hvilken den bindes ved Hæfterødder. Fra Epifyterne afviger Rodklatrerne ved at have Rødder i Jorden. Nogles Rødder kan ligesom Slyngtraade rulle sig om Støtterne (*Vanilla*, *Clusia*). Assimilatorerne er ofte dorsiventrale med siddende Rundblade. De blomstrende kan være forskellige fra de sterile.

### 4. Orden. **Pirrelige Klatreredskeer** af forskellig Art.

Kroge, der ved Berøring pirres til forøget Vækst paa den ene Side; Uhrfjeder-Ranker, d. e. tynde, bladløse Blomsterstandsakser, som er indrullede lig en Uhrfjeder, og som vokser i Tykkelse, naar de griber om en Gren; pirrelige Bladstilke (Arter af *Tropæolum*, *Clematis* o. a.); pirrelige Bladplader (*Fumaria*, *Corydalis*); typiske Slyngtraade, der kan være saavel Dele af Blade (*Vicia*, *Lathyrus*, *Cobæa*, *Gloriosa*, *Smilax*) som Stængler (*Vitis*, *Passiflora*); Hæfteskiver (*Ampelopsis Veitchii*).

Der er ikke skarpt Skel mellem disse 4 forskellige Typer af Assimilatorer; de kombineres i det følgende med de hos Autofyterne sædvanlige Grundformer for Livsformerne i den sædvanlige Rækkefølge: A. Urter, a) Hapaxanther, b) Pollakanther. B. Vedplanter, a) Sublignoser, b) Perlignoser osv.



### A. Urter (Herbæ).

1. Hapaxanther. Om bienne og plurienne forekommer, er mig ubekendt: der findes vist heller ikke Rodklatrere, men derimod de andre Typer, f. Ex.:

Halvlianer. *Galium aparine*. — Af Slingplanter findes mange: *Ipomæa*, *Polygonum*, *Phaseolus*, *Thunbergia* o. a. — Pirrelige Gribeorganer: Arter af *Tropæolum*, *Corydalis*, *Maurandia*, *Pisum*, *Vicia*, *Lathyrus* o. a. Papilionaceer, Cucurbitaceer. I det hele taget er der en Mængde sommerannuelle Arter indenfor de to sidstnævnte Kategorier.

2. Pollakanthe Urter uden Oplagsorganer eller Vandreskud. Sem-pervirente. — Halvlianer. I Troperne f. Ex. Bregner (*Lygodium*, *Gleichenia*), Selagineller, Lycopodier, *Asparagus* osv. — Slingplanter, f. Ex. *Hoya carnosa*, Arter af *Ceropegia*, *Sarcostemma viminale*. — Rodklatrere: En Del Araceer (*Philodendron* o. a.). *Vanilla* (nogle Arter er bladløse), *Begonia fruticosa*, *Pelargonium tetragonum* o. fl. Der er aabenbart ogsaa Arter, som kan være baade Rodklatrere og ægte Epifyter. — Løvskiftende. — Halvlianer, f. Ex. *Rubia tinctorum*, *Galium elongatum*, *Veronica scutellata*, *Boerhavia pentandra*. — Slingplanter: *Humulus lupulus* som Type, *Polygonum dumetorum*, *P. baldschuanicum*, *Pharbitis hispida*. — Pirrelige Organer har en Del Papilionaceer, endvidere *Ecchremocarpus scaber*, *Cobæa scandens* o. a. og maaske ogsaa *Cissus cactiformis*, hvis kødfulde Stængler er bladløse.

3. Pollakanthe Urter med Oplagsorganer (Knolde, Løg). En Del pollakanthe og løvfældende Urter blandt Klatreplanterne har Oplagsorganer af forskellig morfologisk Bygning, nogle overjordiske, andre underjordiske. De forskellige Typer af Klatreplanter er repræsenterede.

Om Halvlianer med Oplagsorganer findes, er mig ubekendt. — Derimod er der typiske Slingere med Knoldrødder, saasom *Ipomæa batatas*, *Exogonium purga* — eller med kartoffellignende Stængelknolde: *Boussingaultia baselloides*, *Dioscoreaceæ* (*Dioscorea*, *Tamus*, *Testudinaria*), *Anredera scandens*, *Jatrophia*, Arter af *Ceropegia*, *Gloriosa*, *Merendera*. — I større Tal er de pirrelige Klatreplanter repræsenterede, med Slingtraade *Cucurbitaceæ* (*Bryonia*, *Rhynocarpa*), *Gloriosa*, *Merendera*.

Løg synes meget sjældne hos Klatreplanter, men findes i alt Fald hos den slyngende, næsten bladløse *Bowiea volubilis* (*Liliaceæ*).

4. Klatrende Urter med Vandreskud. Af saadanne findes aabenbart mange indenfor de forskellige Pollakanther. Nogle er allerede nævnt, f. Ex. Slingplanten *Humulus lupulus*, der har baade Lys- og Jordudløbere. Lysudløbere, hvis Spids tilsidst borer sig ned i Jorden, har *Polygonum cilinode*.

### B. Vedplanter; Xyloideer.

At skelne skarpt mellem Urter og Vedplanter indenfor Klatreplanterne er aldeles umuligt. Lige saa lidt er det muligt at sætte skarpt Skel mellem Sublignoser og Perlignoser. Dertil kommer, at Literaturens Oplysninger ofte er meget vage og ufuldstændige, især naar det drejer sig om de tropiske Klatreplanter, der jo saa

sjældnen kultiveres i botaniske Haver. Mit Forsøg paa en Adskillelse i Typer maa derfor i mangt og meget hvile paa et Skøn og paa det ufuldkomne Kendskab, jeg har til Typerne fra mit eget Ophold i Troperne.

**Sublignoser.** 1. Uden særlige Oplagsorganer eller Vandreskud. Til Halvlianerne vil jeg henregne Arter af *Rubus* og *Rosa*, *Fuchsia integrifolia*, Arter af *Pelargonium* (Sydafrika). I de brasilianske Skovbryn findes mange Compositæ (Arter af *Mikania*, *Eupatorium*, *Baccharis*, *Chuquiragua* og mange andre (se WARMING: Lagoa Santa 1892). I Troperne findes endvidere mange Leguminoser, Rubiaceer, Scrophulariaceer, Solanaceer osv. De klatrende Gramineer (visse Bambuseer) og Cyperaceer (*Scleria*) bør vist ogsaa mindes her. Ligeledes de insekttædende Typer *Nepenthes* og *Dischidia* (maaske nærmest Epifyt). Herhen kan formentlig ogsaa de store Klatreplanter af Slægterne *Ruscus*, *Semele*, *Danaë* og *Smilax* føres. — 2. Nogle Sublignoser har Knoldrødder, f. Ex. Arter af *Smilax*, *Myrsiphyllum*, *Asparagus*.

**Perlignose Klatreplanter.** Her synes alle Skudformer at være repræsenterede, navnlig de mærkværdige, der er forsynede med pirrelige Griberedskaber. Stænglerne bliver hos mange tykke, stærkt forveddede og med yderst usædvanlige anatomiske Bygningsforhold. Det er især de mægtige, højt klatrende Arter, der har Navnet »Lian«.

**Halvlianer.** Herhen Slægten *Bougainvillea* og de Palmer, der benævnes »Rotang«, og som har Flageller. Hvis man ikke vil medtage alle Bambuseer under Poioideer, bør nogle føres herhen.

**Slyngplanter.** Vi har en udmærket Type i *Lonicera periclymenum*, der har urteagtige Knopskæl, endvidere *Aristolochia Sipo*, Arter af *Menispermum*, *Asclepiadaceæ*, *Hydrangea* osv.

**Rodklatrere.** *Hedera helix* er typisk. Stammerne kan blive meget tykke, de klatrende Skud er plagiotrope og sterile, de blomstrende rodløse, oprette, negativ geotropiske og har anden Bladform. Til *Hedera* slutter sig Arter af *Marcgravia* og *Ficus* med de samme Ejendommeligheder. Fremdeles er her en Mængde andre tropiske Rodklatrere, som nævnes af SCHENCK og TREUB.

Pirrelige Gribeorganer er rigt repræsenterede i Troperne. Slyngtraade har mange Arter af *Smilax*, *Ampelopsis*, *Vitis*, *Bignoniaceæ*, *Passifloraceæ* og *Sapindaceæ*. Pirrelige Bladstilke har Arter af *Clematis*. Pirrelige Kroge, der er smaa Aksel-skud, hos flere Rubiaceer og Anonaceer.

Uhrfjederranker træffes hos visse Rhamnaceer, Sapindaceer og Bauhinier. Klatreplanter med Hæfteskiver eller Hæftekløer har flere Ampelidaceer, Bignoniaceer (f. Ex. *Glaziovia bauhiniopsis*); endvidere *Pithecolobium phaseoloides*, *Bauhinia capreolata*.

Som tidligere nævnt, mangler der om de allerfleste i Literaturen nævnte tropiske Arter mere detaillerede Oplysninger; et Udtryk som »frutex scandens« er ganske utilstrækkeligt til at kunne anbringe den paagældende Plante paa rigtigt Sted i Systemet.

Flere Arter kan optræde med forskellig Type. Omkring Lagoa Santa findes Arter, der i Skovene optræder som Klatreplanter, i Campos serrados som oprette Perlignoser (Buske) med kraftige Langskud, der ikke klatrer. SCHENCK omtaler lignende Fænomener. De har den store Interesse, at vi derved føres ind paa Spørgsmaalet om Oprindelsen af Klatreplanternes mærkelige Ejendommeligheder, som maa siges endnu at være meget gaadefulde.

## VIII.

### Allotrofer (Heterotrofer).

Som omtalt S. 124 bør det første store Skel i Livsformernes System sættes mellem Autotrofer og Allotrofer; de første optager al deres Næring, i det mindste som ældre, fra uorganiske Forbindelser i Luft, Vand og Jord, medens de sidste i større eller mindre Udstrækning og ad forskellig Vej optager organisk Næring, enten fra livløse, organiserede Rester af Planter eller Dyr (Saprophyter) eller direkte fra levende Organismer (Parasiter).

Autotrofe er alle grønne Planter (de fleste Alger, Mosser, Karkryptogamer og Fanerogamer) og enkelte ejendommelige Bakterieformer. Allotrofernes langt overvejende Mængde udgøres af Bakteriernes og Svampenes Hærskarer, hvortil slutter sig et Faatal af farveløse (klorofylfri) Planter fra de ovenfor nævnte Grupper. Skellet er som omtalt S. 125 dog ingenlunde skarpt, idet der næppe eksisterer nogen Planteart, som ikke paa et vist Tidspunkt af sit Liv er mixotrof, da den (ved Kimdannelsen eller ved Spiringen af Frø eller Sporer) maa ernære sig af organisk Næring ved Siden af den uorganiske. Der er meget stor Forskel paa, hvor indgribende Betydning for en Organisme den ene og den anden Slags Næring har. Der er Exempler paa fakultativ og paa obligat Allotrofi. I hvilken Grad Arterne kan være nøje knyttede til en bestemt Standplads og en bestemt Næring og tilpassede til dennes Natur — altsaa Kausalsammenhængen mellem Form, Ernæringsmaade og Standplads — ses næppe noget Sted tydeligere end hos Allotroferne. Specialiseringen føres f. Ex. hos visse Svampe saa vidt, at de kun kan benytte ganske enkelte Sukkerarter som Kulstofnæring og hos enkelte Fanerogam-Parasiter træffes det mærkelige Tilpassningsforhold, at deres Frø kun spirer, naar de befinder sig i umiddelbar Nærhed af en egnet Værtplante. — Men dette mægtige og forøvrigt saa interessante, men ogsaa vanskelige biologiske Kapitel kan jeg her kun yderst kort berøre. Specialisterne maa uddybe det nærmere.

#### 16. Klasse. Saprophyter.

Mixotrofer. Saaledes som tidligere nævnt, er Grænsen mellem Autofyter og Allofyter ikke skarp. Forbindende Overgange mellem de to Grupper danner de mixotrofe Autofyter (Hemisaprophyter). Disse Planter erhverver sig Kulstof væsentlig ved deres klorofylholdige Organer (Assimilatorer), men kan ved Siden af i højere



eller ringere Grad optage kulstof- og kvælstofholdig Næring fra livløst organisk Stof. Foruden mange grønne, som normale Autofyter udstyrede Arter, der hører herhen (Muldbundsplanter som f. Ex. *Listera cordata*, *Dentaria*, *Pyrola*-Arterne, Gødningsplanter som Mosslægterne *Splachnum* og *Tetraplodon*) kan henvises til nogle ejendommelige Typer, som f. Ex. mange Bromeliaceer og visse Bregner, der opsamler Muld og organiske Dele (se S. 142) og til Insektivorerne (af de 5 Familier: *Droseraceæ*, *Sarraceniaceæ*, *Nepenthaceæ*, *Cephalotaceæ* og *Utriculariaceæ*).

Grupperingen af Livsformerne indenfor Allofyterne kan tildels ske efter det samme System, som er lagt til Grund for de autotrofe Planters Inddeling. Man kan f. Ex. sondre mellem Hydatofyter (med Mikroplankton og forskellige Benthosformer) og Aërofyter (herunder Epifytoïder, Chthonofyter osv.). Repræsentanter for alle de under Autofyterne opstillede Typer findes dog næppe, men til Gengæld kommer nye Grupper til i Harmoni med de specialiserede Kaar (f. Ex. Endofyter).

Holosaprophyter. En Mængde Arter ernærer sig af livløst organisk Stof alene (Humus o. a. Stoffer). Blandt dem findes Vandplanter i fersk og salt Vand: Mikroplankton som Bakterier, Flagellater, nogle Phycomyceter eller Benthos (Phycomyceter o. a. Typer). Herhen maa ogsaa kunne føres en Mængde mikrobe Landplanter, der lever i Jorden og har en umaadelig Betydning for dennes Biologi, samt Former, der findes som Endofyter hos Dyr og Mennesker (f. Ex. Bakteriefloreen i Tarmkanalen). Dertil hører desuden en Mængde forskellige Svampe af meget forskellige Typer og af højere Planter nogle faa, bl. a. følgende: *Monotropa*-Typen med stærkt knopskydende Rødder, Arter af *Gentianaceæ*, *Polygalaceæ*, *Triuridaceæ*, *Burmanniaceæ* og en Del Orkideer med forskellig morfologisk Bygning (*Neottia nidus avis*, *Coralliorrhiza innata*, *Epipogon aphyllum*, *Pogonopsis*, *Gastraeda*, som har Knold i Jorden, og flere andre.

### 17. Klasse. Symbiotiske Typer.

Denne anden store Gruppe af Allofyter afviger fra den nævnte første derved, at Arterne er symbiotisk knyttede til andre. Symbiose kan tages i videre og snævrere Forstand og frembyder en Mængde Varianter i Omfang, idet den langt fra altid er lige gavnlig for begge Parter. VAN BENEDEN har som bekendt tre forskellige Trin: 1. Kommensalisme er den ringeste Grad af Symbiose; »Symbionterne« spiser ved samme Bord, men har ellers intet med hverandre at gøre, de hverken skader eller gavner hverandre. — 2. Mutualisme; Arterne gør hverandre gensidige Tjenester. — 3. Parasitisme; den ene Part skader den anden.

Grænserne mellem disse 3 Trin er naturligvis ikke skarpe. Som Exempel paa

1. Kommensalisme i den videste Form kan nævnes Samlivet mellem Arterne i et Samfund, være sig i Vand eller Luft. Her ligger store og vigtige Opgaver for os, som bl. a. Studiet af Livsformerne skulde hjælpe til at løse. Snævrere er Baandet mellem Epifyten og Værten, der giver den Husly; i nogle Tilfælde er Epifyten ganske uskadelig (S. 139); i andre kan den ved at optræde i stor Mængde blive hindrende for Værtens Liv, for dennes frie og normale Udvikling. Paa samme

Maade er Forholdet mellem Klatreplanten og dens Støtte (S. 179), mellem de Planter, som har Domatier (Boliger) paa Blade eller i Stængler og de deri levende Smaadyr (Mider, Myrer). Inderligere bliver Samlivet mellem visse Endofyter, der faar Husly hos Planter, f. Ex. Alger i Hulheder hos *Azolla* eller *Gunnera*.

2. Mutualisme. Det er ofte meget vanskeligt at faa Rede paa Samlivets Natur; saaledes er den baade hos Autotrofer og Allotrofer optrædende Mykorrhizas Nytte for Værten ikke sikkert forstaaet. Mere Enighed er der om, at de mikrob-  
husende, smaa »Mycodomatier« hos Leguminoser, *Alnus* og *Myrica* hjælper Værten til Assimilation af Luftens Kvælstof; men hvad Nytte Mikroberne selv har, er mindre klart. Mest nødvendige er Svampemycelierne for mange Orkideers Spiring (BERNARD o. a.).

Under Mutualisme maa ogsaa henføres det Forhold, at Alger optages i Svampelegemer og maa trælde for Svampen (Helotisme), mens Svampen paa den anden Side ogsaa tilfører Algerne visse Næringsstoffer; kendt fra Likenerne.

3. Parasitisme er i Regelen lettere at kende, fordi den ene af Parterne gør den anden Fortræd. Mange Parasiter er saa afhængige af deres Vært, at de kun kan trives paa een enkelt Art; andre kan tage Næring af forskellige Arter. Alle Parasiter maa i større eller mindre Grad være Endofyter; »Ektoparasiterne« trænger kun med en lille Del af deres Legeme ind i Værten, »Endoparasiterne« lever helt inde i Værtplanten. Nogle Arter kan leve baade som Saprophyter og Parasiter. Klassen omfatter mange forskellige Typer.

1. Halvsnylttere (Hemiparasiter). Snylteren har Klorofyl. Den maa altsaa selv kunne assimilere Kulsyre og modtager kun kvælstofholdige Stoffer og uorganiske Salte fra Værtplanten.

Typer: *Loranthaceæ* (S. 176), *Santalaceæ*, flere *Rhinanthoideæ* (*Pedicularis*, *Bartsia*, *Rhinanthus*) med baade enaarige og fleraarige Arter.

2. Helsnylttere (Holoparasiter) har ingen Klorofyl og er udelukkende hen-  
vist til at ernære sig ved Værtens Hjælp.

Snyltende er mange Bakterier og bakterioide Typer; endvidere mange Svampe (*Peronosporaceæ*, *Ustilaginaceæ*, *Uredinaceæ* osv.), som snylter ved Mycelier, mange snyltende Blomsterplanter: 1. Paa Rødder af Værtplanterne snylter f. Ex. *Lathræa*, *Orobanche* (polycyklisk), *Balanophoraceæ*, *Hydnoraceæ*, *Rafflesiaceæ*. 2. Paa Assi-  
milatorerne snylter f. Ex. *Pilostyles*. 3. Sluttelig er der de »lianoïde« Snylttere: *Cuscuta* og *Cassytha* (af Fam. *Convolvulaceæ* og *Lauraceæ*) med baade enaarige og fleraarige Arter.

Allotroferne yder mærkelige Exempler paa Tilpasning og paa, at Organer, som er blevet overflødige til Livets Førelse, falder bort. Kulsyre-Assimilationen er op-  
hørt hos Holosaprophyter og Holoparasiter; i Overensstemmelse hermed forsvinder Løvbladene med alle deres Epharmonier samtidig med Arbejdet; de gamle Organer undergaar en tilbageskridende Udvikling, idet nye fremstaar, eller de forsvinder helt.

Smukt ses denne tilbageskridende Udvikling f. Ex. hos *Rhinanthus*-Gruppen indenfor *Personatae*; her findes en Række Slægter med grønne Hemiparasiter (*Euphrasia*, *Melampyrum*, *Rhinanthus*, *Pedicularis*), hvis Arter efter HEINRICHER er bundet til et snyltende Liv; Yderfløjen dannes af Helsnylteren *Lathraea*.

Vidnesbyrd om, at Bladgrøntets Forsvinden staar i direkte Forbindelse med Tilgang af organisk Næring giver Diatomeer, som lever paa Bund med raadnende Stoffer og hvis Kromatoforer bliver farveløse, eller Alger, der kommer til at leve i Saftflod af Træer, som er rige paa Kulhydrater, eller dyrkes i Vædske med Druesukker, Glycerin eller anden organisk Næring — de bleges og forvandles fysiologisk set til Svampe; den paa *Rhodomela* levende lille knoldformede Rødalge *Harveyella mirabilis* har ifølge KUCKUCK ingen Kromatoforer og er en ægte Snylter.

Indirekte vidner mange Arter om den samme forenklende Udvikling fra Autofyt til Allofyt, idet der indenfor nærstaaende Grupper findes begge Slags Livsformer. Exempelvis kan anføres, at typisk autotrofe og typisk allotrofe Slægter findes indenfor Flagellaterne, hvor stærkt omdannede Slægter kan paralleliseres med uforandrede, f. Ex. *Astasia* med *Euglena*, *Polytoma* med *Chlamydomonas*, *Chilomonas* med *Cryptomonas*; hver af disse tre allotrofe Slægter lever paa Steder, hvor Æggehvide-stoffer raadner, og hver af dem har sin særlige Kvælstofkilde.

Flere allotrofe og autotrofe Paralleltyper nævnes i det følgende: *Cuscuta* og *Convolvulaceæ*, *Cassytha* og *Lauraceæ*; blandt *Gentianaceæ* *Voyria* i Amerika, *Cotyl-anthera* i Asien, nær op til *Pirolaceæ* de saprofyte *Monotropa* og *Sarcodes*; blandt de autotrofe Burmanniaceer de saprofyte *Thismia* og *Baynesia*; blandt Orkideerne f. Ex. Saprofyterne *Coralliorrhiza*, *Epipogon*, *Neottia*, *Pogonorchis*, *Wulfschlagelia* o. a.; nær *Narthecium* Parasiten *Petrosavia* osv.

Allotroferne er sent udviklede Typer, der ikke danner nogen enkelt, sammenhængende Udviklingsrække, men optræder spredt omkring i hele Systemet, smaa Udviklingslinier, tilpassede til helt andre Ernæringsforhold paa lige saa fuldkommen Maade som Autofyterne, om end i flere Henseender morfologisk og anatomisk forenklede. Der er Arter, som kan leve baade som Parasiter og som Saprofyter, og ofte er Udviklingen formentlig gaaet gennem Epifyter eller Klatreplanter eller Endofyter til fakultative Saprofyter, obligate Saprofyter og derfra videre gennem først fakultative og indifferente Parasiter til obligate og specialiserede Helparasiter.

I denne tilbageskridende Udvikling er det som nævnt først og fremmest de kulsyreassimilerende Organer, som omdannes, en naturlig Følge af, at det er Ernæringsmaaden, som forenkles. Men ogsaa Rødderne omdannes; i Stedet for typiske Rødder kommer ofte Rhizoïder eller Mycelie-lignende Organer, der trænger ind i Værtens Væv og fra dette optager kvælstofholdige Stoffer og anden Næring. Parallelt med Reduktionerne i det ydre gaar Forenklinger i den indre Bygning. Styrkevæv udvikles ikke og Ledningsvævet er ofte svagt.

Ligeledes bliver Frøene smaa; men til Gengæld meget talrige, i Overensstemmelse med, at kun en meget lille Brøkdelen naaer til den specielle Standplads, som



Artens normale Udvikling kræver. Kimen er meget lille, udifferentieret, og ved Spiringen anlægges Organerne sent (der dannes en »Protokorm«).

I denne Udviklingsgang fra Autofyt til Allofyt er det de edafiske Forhold, som har den største Rolle, i ringe Grad eller slet ikke Varme, Lys og Fugtighed. Forplantningsorganerne behøver ikke at paavirkes, men Exempler findes paa, at ogsaa disse (Blomsterne) gennemgaar en saa gennemgribende Omdannelse, at Arternes Plads i Systemet bliver ganske uklar (f. Ex. Rafflesiaceerne).

Ikke nogen anden Række af Livsformer synes i den Grad at vidne om, hvor stærkt Arternes Former og Liv er tilpasset til, afhængig af de Kaar, under hvilke de lever, og hvilken Betydning den direkte Tilpasning spiller for Oprindelsen af nye Arter.

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Anm. Da jeg paa Grund af Sygdom er bleven forhindret i selv at læse Korrekturen paa denne Afhandling, er Størstedelen af den besørget af Professor Kolderup Rosenvinge og Stud. mag. C. A. Jørgensen. Jeg bringer herved mine to udmærkede Hjælpere samt Redaktøren en hjertelig Tak for den gode Støtte, de har ydet mig ved dette vanskelige Arbejde.

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CONTRIBUTIONS  
TO  
THE BIOLOGY OF THE ROTIFERA

I. THE MALES OF THE ROTIFERA

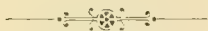
BY  
C. WESENBERG-LUND

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WITH 15 PLATES AND 17 TEXTFIGURES

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D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATHEM. AFD., 8. RÆKKE, IV. 3



KØBENHAVN  
HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL  
BIANCO LUNOS BOGTRYKKERI

1923





## Introduction.

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From the moment when the microscope was invented, the Rotifera have interested the naturalists in a very high degree. They were studied by the great naturalists of the eighteenth century together with the innumerable unicellular organisms which, in a single drop, were brought under the microscope in many hundreds of specimens. As well known, our own countryman O. F. MÜLLER (1786) has contributed in a very great degree to the study of these charming little creatures. Even if some of these old naturalists had a conception that Infusoria and Rotifera really only were identic with regard to size, but differed very much from each other in all essential points, they were actually, until 1838 when EHRENBERG's famous work arrived, treated in the same great division of lower organisms, which the different authors gave very different names.

It was EHRENBERG who was the first to definitively separate the Rotifera from the Protozoa; as of course at the then existing stage of science he could have no idea of the fact that the first group comprised multicellular, the other unicellular organisms, he had also no idea of how great the gulf between the two divisions really was. The word Protozoa was first formed by v. SIEBOED in 1845, the word Metazoa by HAECKEL, and he is really the first to contrast the Protozoa with "die Gewebetiere" (Metazoa). Until 1838 all described and figured Rotifers have most probably only been females. Almost all the hundreds of Rotifers which EHRENBERG figured and described in such an admirable manner were females. But EHRENBERG did not regard them as such, but as hermaphrodites; according to him the excretory organ with the lateral canals and contractile vesicle were the male organs. It was later on shown that two of his Rotifers, *Enteroplea hydatina* and *Notommata granularis*, were really Rotifer males, but he was so convinced of the correctness of his view of the hermaphroditic character of the group, that the two above named males, the first-named the male of *Hydatina senta*, the last-named the male of *Brachionus pala*, were described as Rotifers, quite like all the other Rotifers and regarded as hermaphroditic like these. Already the naturalists of the time in which EHRENBERG lived, understood that the organs which EHRENBERG described as male organs, could not be interpreted as such; on the other hand true male organs could not be found. In his "Vergleichende Anatomie" SIEBOED (1848, p. 184) is therefore forced to confess: „Trotz der sorgfältigsten Bemühungen hat sich bis jetzt kein befriedigendes Resultat

über die wahre Beschaffenheit ihrer männlichen Geschlechtswerkzeuge erzielen lassen, so dass es noch zweifelhaft ist, ob die Rotatorien Hermaphroditen sind oder getrennte Geschlechter besitzen." —

It was BRIGHTWELL who in 1848 was the first to find a male of the Rotifera and regard it as such. In 1849 it was more thoroughly described by DALRYMPLE. It was the male of *Asplanchna Brightwelli*. In 1850 GOSSE (p. 18) described the male of *A. priodonta*. In 1851 WEISSE (p. 347) described the male of *Diglena catellina*, but did not regard it as such, describing it as a new species, *D. granularis*. In 1854 a LEYDIG (p. 99) supposed that the above named two species, *Enteroplea hydatina* and *Notommata granularis*, and further the *D. granularis* of WEISSE were really all males of Rotifers: he gave exhaustive reasons for his suppositions, but was not able to prove them; he however described the male of *Asplanchna Sieboldi* simultaneously. In 1856 COHN found the male of *Hydatina senta* and showed that LEYDIG's supposition was correct and that the *Enteroplea hydatina* of EHRENBERG was really the male of *Hydatina senta*. In 1857 LEYDIG (p. 404) himself found the *Hydatina* male and gave valuable contributions to the anatomy of this animal. Already in 1858 GOSSE's paper: *On the Dioecious Character of the Rotifera* appeared. In this paper 10 Rotifer males were described: of these the seven were really the males of *Brachionus*, the others belonging to *Polyarthra platyptera*, *Sacculus viridis*, and *Synchaeta tremula*(?).

With this paper the common dioecious character of the whole group was really demonstrated; curiously enough, during the following forty years only very few males were observed; and if they were observed, they were almost always insufficiently described and very badly drawn. Even the large work of HUDSON GOSSE, with regard to the structure of the males, was hardly of any significance at all. From these forty years there exists only a good description and drawing of *Euchlanis dilatata* (COHN 1858) and of *Copeus pachyurus* (DIXON-NUTTALL 1894). Further, PLATE has (1886 a) contributed to the study of the males of *Brachionus*, *Hertwigia*, *Polyarthra*, *Triarthra* and *Asplanchnopus*. HUDSON-GOSSE (1886) described the exterior of the male of *Pedalion*; of the other males mentioned in the work the drawings and descriptions are very insufficient. From this period several papers relating to the structure of the males certainly appear (METSCHNIKOFF 1866: *Apsilus*; DADAY 1883, 1891: *Asplanchna*; MILNE 1885: *Diglena*; WESTERN 1888: *Asplanchnopus*; *Gastropus clavulatus*; 1892 *Triphylus lacustris*; *Asplanchna* 1890; THORPE 1889: *Megalotrocha*; ANDERSSON 1889: *Megalotrocha*; ROUSSELET 1892 b *Conochilus*, 1894 *Cyrtosia*; DIXON-NUTTALL: *Stephanoceros* 1896). But almost all these males are very insufficiently drawn; generally the authors confess that they have only seen a single male and that it died before further observations could be made.

In the time from 1896—1908 a series of very valuable papers appears and our knowledge of the structure of the males is much augmented. ROTHERT (1896) and ROUSSELET (1897 d) study the males of *Proales Wernecki*. WEBER (1897—1898) gives a series of excellent drawings of males several of which have never been found



again later (*Salpina*, *Colurus*, *Dinocharis*, *Diglena*, *Scaridium*, *Hydatina*, *Copeus*, *Colurus*). Almost simultaneously ROUSSELET's descriptions of *Rhinops* (1897 a) and of *Plerodina* (1898) appeared. Very exhaustive descriptions and elaborate drawings are furnished by MONTGOMERY of the males of *Floscularia proboscidea* (1903), by HAMBURGER of *Lacinularia socialis* (1907) by KRÄTSCHMAR of *Anuræa aculeata* (1908) and by DE BEAUCHAMP of *Eosphora digitata* (1905). In 1903, ROUSSELET (p. 172) gives a list of all known Rotifer males, indicating more than 100. Very many of these males have however only been observed, neither described nor drawn. Simultaneously with these papers others appear in which males certainly are described but often in such a manner that it is almost impossible to recognise them; this especially holds good with regard to the descriptions and drawings by WECHÉ and MARKS & WECHÉ (1902 and 1903). Even in this period very valuable monographs on different families of Rotifera appear, especially ROUSSELET's on *Synchæladæ* (1902), DIXON-NUTTALL's on *Diaschiza* (1903), JENNINGS on *Rattulidæ* (1903), HLAVA on *Meliceritidæ* (1908 a). Whereas these monographs augment our knowledge very much with regard to the females, the males are either not mentioned at all (*Rattulidæ*) or only rather cursorily mentioned and figured. Apart from a very superficial drawing and description of *Anuræa aculeata* by MONTET (1915) after 1908, as far as I know, no new males are described.

If now we will try to collect in a few lines our present knowledge with regard to the males of Rotifers it may be expressed as follows. Of the more than 1000 Rotifers described the males have only been observed in a little more than 100 species, but of these scarcely one score may be said to have been more exhaustively studied. Of the 25 families of Rotifera the males are wholly unknown in eight (*Philodinidæ*, *Adinetadæ*, *Microcodidæ*, *Rattulidæ*, *Gastropodidæ*, *Ploesomatidæ*, *Cathypnadæ* and *Anapodidæ*). In several of the others which contain a large number of species, only the male of a single one or a few has been observed and often only once. The male of the most common Rotifer *A. cochlearis* is unknown. This in other words means, that our whole present knowledge of the Rotifera has hitherto been built almost exclusively upon the female sex; further that all systematical arrangement of the group has only been tried with regard to this very sex. This rather peculiar result of so many exhaustive and elaborate studies, carried on for about two hundred years and most probably almost unique in the history of Zoology, is due to a series of very intelligible factors.

The males are generally regarded as very rare, much rarer than the females; this may really be true for several genera and perhaps families, but according to my experience only for relatively few; the fact is that the males appear only in strongly marked periods in the lifetime of the species; these periods are bound to fairly fixed seasons of the year, the so-called sexual periods, which for many species occur twice a year, in spring and autumn, for others only once a year, and then almost always at the highest summer temperatures; in a few cases during the winter season, and then even at temperatures near zero, below the ice. The first-named species are termed polycyclic, the others monocyclic. Almost simultaneously LAUTERBORN and myself have tried to elucidate the periodicity of the Rotifera; LAUTERBORN's papers appeared in

1893—1900 just at the period when mine should have been printed; as the results of the researches were almost quite congruent, I provisionally retracted most of my paper, but have carried on my investigations to this very day. Every year it became more and more obvious how difficult it really was to get a clear understanding of the phenomena and how necessary it was to extend the investigation over as long a time as possible. During the long period from 1898 to 1920 these investigations have not always been in the foreground. Those who know the publications from this laboratory, will be acquainted with a series of investigations, which have nothing to do with the study of Rotifera. As however very many of the investigations have been carried on in ponds and moors, and I have almost always had a Rotifer net with me, a lot of rather casual observations have been gathered. It was noted when rather rare Rotifers were observed in the different ponds, and when maxima or sexual periods were detected. The material which was collected in this way and which was derived from more than twenty years of observation, originated from many hundreds of ponds, lying partly in North, partly in Middle Seeland, mainly with a radius of only a few kilometers from the laboratory.

Firstly my attention was directed towards the study of the periodicity of the Rotifera; simultaneously herewith, I had ample opportunity of getting to know a long series of males, and I saw how many of them had never been described. I therefore made a great many notes with regard to their occurrence. Simultaneously herewith a great many cursory drawings and notes relating to the males were made. When all this material was collected and overlooked in 1919, it was clear that it contained many new males and many new observations relating to males hitherto slightly known. A monographical treatment of the males of the Rotifera was then planned. From the many separate casual observations from the foregoing years I was able to begin the investigations upon a long series of fixed localities and upon fixed times. From the earlier observations I knew exactly when and where I might expect to find the males of very many Rotifers. In the spring of 1920 these studies were the chief aim of the laboratory. — In very many cases my calculations were correct, but there were of course also cases where it was impossible to find the species seen many years before. What has been in a very high degree unfortunate for the investigation is the devastation of so very many small ponds, either lying in the fields or in the forests, and which cultivation has either totally closed or filled with material that has killed the fauna. However, if I had not had the preliminary investigations of the years 1900 to 1920 as a support, it would unquestionably have been quite impossible for me in the course of only two years of observation to procure sufficient material for drawing about fifty Rotifer males. Most of the authors who have studied the group for a long series of years have commonly only seen a glimpse of the males of very few species. The now published investigation gives camera-drawn figures of 45 males; of these males more than twenty are quite new to science and eight belong to families in which males have hitherto been wholly unknown. Many of the other males here described and figured

have been observed at an earlier date, but are often mentioned in the literature only in few words and are very insufficiently drawn.

It would by no means have been difficult to increase the number of the now published males considerably; in all those cases where I have not been fairly sure of the determination, or where I have been unable to distinguish the males from other described males, they have been omitted. This has especially been the case with the males of the fam. *Notommatidae*, *Flosculariade*, *Synchaetade* and *Brachionidae*.

In the present stage of knowledge we still lack every acquaintance with the males of the families *Philodinidae*, *Adinetade*, *Microcodidae*, *Cathypnadae* and *Anapodidae*. Simultaneously with the preliminary investigations, a long series of papers appeared which were the results of very many exhaustive and excellent studies, relating to sex determination, mainly studied in Rotifera. Even if the chief object of these investigations was by no means to elucidate the cyclic propagation of the Rotifera, they gave a long series of contributions which were of the greatest significance to the elucidation of all problems relating to this difficult matter; most of these investigations were carried out in North America. First it troubled me greatly that all the results, gained in this way, were in the most striking contradiction to all that I saw; and for years I saw no means of bringing the results from the laboratory investigations in harmony with those carried out in Nature. The laboratory investigations were almost all carried on upon *Hydatina senta*, partly upon *Asplanchna* and *Proales*, and it was only after I had found in Nature the natural conditions under which these species lived, and regular observations had begun here, that it was possible for me to understand how the differences were to be interpreted.

In this first part of the work I only wish to describe and figure the males, give a general sketch of their anatomy, and contribute to the understanding of the phenomenon, unique in the animal kingdom, that the one sex of the species in a whole group of animals, counting more than 1000 species, all without any parasitic phenomena, and living side by side with the other sex, in some cases is subject to such an enormous reduction, that it is merely reduced to swimming testes "perambulating bags of spermatozoa" (ROUSSELET 1897 a, p. 6), surrounded by a thin cuticula, on its anterior part covered with a bunch of cilia; we have here to do with freeswimming metazoa with the number of cells most probably smaller than in any other organism in the animal kingdom, with a size not greater than a few times that of a blood corpuscle, which pair at the very moment of birth and most probably in some species die in almost the same hour in which they are born.

Before entering upon the description of the males, it will be necessary to give a preliminary sketch of the localities from which I have gathered the material; the results with regard to the sexual periods, as they manifest themselves in nature under natural conditions; further of the methods I have used for the study of the males and lastly, a short view of my systematic conception of the whole group.



All the investigations have almost exclusively been carried on in ponds not in lakes. It is a well-known fact that the Rotifera really form a rather prominent part of the lake plancton. But the investigations have also shown that from the plancton of lakes we only know extremely few, perhaps not a single Rotifer, which is not also to be found in the pond plancton: even *Ploesoma Hudsoni*; *Gastropus stylifer* are pond forms; here in the ponds the maxima are much more pronounced than in the lakes. It is also a well-known fact that many of the colonies of the most pronounced plancton Rotifers from the pelagic region of larger lakes only rarely carry resting eggs, and that it seems that we often have to do with acyclic colonies. The pelagic region therefore is not the right spot for those who wish to study the males of the Rotifera.

The Rotifer life in ponds may of course be divided into a series of rather different societies or associations. Any one who wishes to get an idea of the Rotifera of a pond need only reckon with three associations viz. the Rotifer life in the central part of the pond, free from vegetation, "the pelagic" fauna; the creeping or swimming Rotifer fauna of the vegetation, and the fixed Rotifer fauna. Each of these faunas may be collected by special apparatus, and in different ways, the first by means of plancton net Müllergaze No. 20, the second with a plancton net Müllergaze No. 15, provided with a sieve to keep back the algæ. These two nets are provided with a cord of about 10 meter and are used as throwing nets; the fixed fauna is best gathered by means of a net, placed upon a 1 meter long stick. — For the study of the "pelagic" fauna a boat is always desirable. — A special Rotifer fauna strongly associated with ponds of quite a special type cannot, according to my experience, as a rule be pointed out; the single exception is the Rotifer life in ponds which dry out early and only possess water for a month or two after the ice has melted; especially if these ponds are simultaneously polluted by dark water from dunghills, we shall find quite a special fauna with *Hydatina* and some species of *Notommatidae* as the most characteristic Rotifer forms in them. A special Rotifer fauna only associated with peaty water does not exist; some species, viz. *Pedalion*, occur mainly in localities of this nature, but this species may also be found in ponds with clear most probably chalky water. It is of interest that the different holes in a peat moor often contain a very different Rotifer fauna simultaneously.

Any one who wishes to become acquainted with the Rotifer fauna of a locality, must further remember always to take a series of samples, as far as possible at regular intervals, best every week; a single sample has only very little scientific value. The Rotifer fauna differs from week to week; this especially holds good with regard to the "pelagic" Rotifer fauna; for any one who wishes to study the periodicity, the temporal variations, the occurrence of sexual periods etc., this manner of proceeding is of course a *conditio sine qua non*. In the time from 1900 to 1920 regular observations have been carried on in very many ponds or smaller lakes; the researches which are now going to be published, make use of twenty-two series of ob-

servations, carried out in twenty-two different smaller lakes and ponds and accomplished in 12—16 months with intervals of eight to fourteen days.

I am inclined to think it a tacit supposition that the Rotifer life in ponds is almost totally obliterated during the winter half-year, and that the many different species all spend the winter as resting eggs; this is a very great mistake. Very many species, belonging to all the three above-named associations, may be found at temperatures very near zero, and in those cases where I have been able to study the life in ponds which have been iced, I have found at airtemperatures of  $\div 10^{\circ}$  C., even if the pond was icebound for a month, almost quite the same pelagic Rotifer fauna as before the pond was icecovered.

The sexual periods manifest themselves not so much owing to the presence of the males which, because they are so exceedingly small, are almost always overlooked, but much more owing to the presence of the dark resting eggs which on the one hand are the result of the pairing process, on the other hand cannot be formed, if a pairing process does not take place, the presence of which therefore indicates the point of time when the males have appeared.

A long series of investigations carried on from this laboratory have shown that in the different species of Rotifera the sexual periods differ very much with regard to strength and distinctness. There are species which year after year have very pronounced sexual periods simultaneously in very many localities and in which the males in these sexual periods occur in millions, other species where the sexual periods almost always and everywhere are very little pronounced, and which mainly seem to propagate parthenogenetically. In all these species the number of males in a given locality is exceedingly small. Finally, there are species in which sexual periods have never been observed, and which really seem to propagate parthenogenetically the whole year round. The investigations have further shown, that just those species in which pronounced sexual periods in very many localities appear almost simultaneously, when appearing under special conditions, here seem to be almost acyclic i. e. without pronounced sexual periods. This is the case with those species which are not only to be found in the plankton of smaller ponds, but also occur in the pelagic region in larger lakes. These species may in the ponds be di- or polycyclic, whereas as plankton organisms in the larger lakes they are monocyclic, or for several years even acyclic.

It will be understood that, when hunting for Rotifer males, it is of the greatest significance to know, when the sexual periods for the different species occur; then only, in these often very sharply defined periods, the males occur. If however we only use the resting eggs as indicators of a sexual period, we shall very often be too late to get the males; the life of the males is often restricted to only a few hours and is sure never to last more than four or five days; as these days for the total amount of specimens of a given species almost coincide and are only rarely distributed over more than about 10 days, and as further the resting eggs appear in the last part of this period and are often carried by the females for rather a

long time, it will be understood that the males have commonly disappeared when a colony mainly carrying resting eggs has come under observation. Stress must therefore be laid upon the point of tracing a sexual period before it comes. To do this we possess different means.

It has in an earlier paper (1898) been shown that, before a sexual period sets in, the species in a given locality will very often increase enormously in number. The species attains to what we commonly call its maximum. This observation has been corroborated by almost all later authors.

The magnitude of these maxima differs very much from species to species; for the same species they are neither of the same magnitude in different localities, nor in different years in the same locality. In the same locality they may be displaced a little from year to year, but all in all they occur at rather fixed seasons; competition with other species, climatic conditions, variation in nourishment determine the magnitude. If the general conditions are of such a kind that they cannot develop at the time which may be regarded as the natural one, the maxima as far as my experience goes are not developed that year; a compensation later on in the year very rarely takes place.

The maxima are almost always greatest and most conspicuous in the "plankton society". They may be so large, that the said Rotifers determine the colour of the water. This f. i. was the case with some of the ponds, where *Asplanchna priodonta* had its great maximum; the water was then of a milky appearance; this is however rather a rare case; it is commonly the colour of the chromatophores of the food algae which determines the colour of the pondwater. Especially in spring the maxima in the pelagic pond Rotifers, owing to enormous parthenogenetic propagation, may set in with an almost incredible force; the large females of *S. pectinata* may have seven or eight eggs in the oviduct; *Rhinops* and *Asplanchna* eight or ten young ones and the young ones, before they are hatched, may have half developed young ones in their oviducts. The duration of the maxima differs very much; for some species it is several weeks, for others only six or seven days; they may suddenly be cut off either because of the setting in of a sexual period, or owing to unfavourable climatic conditions. Now and then two or more species have their maxima simultaneously, but commonly they succeed each other; regular observations carried on for years show clearly that the succession, in which they appear in the same pond, is almost the same year after year; most probably the species, with regard to rapid propagation upon which the great maxima of course depend, are bound to the great regular variations in climatic conditions upon which again the amount of nourishment for the Rotifera depends.

With regard to the creeping or slowly swimming Rotifer association, whose habitat is the vegetation zone of perennial ponds, the maxima, according to my experience, are by no means so great; they do not appear with that wonderful regularity which is so characteristic of the plankton Rotifers. Whereas for very many of my ponds I am able to say in what week exactly the maximum of that plankton



Rotifer will begin, I am never able to say the same for the Rotifers from the vegetation zone. With regard to this association, year after year the investigation offers unsuspected surprises. Here, with regard to time as well as to quantity the maxima have an extremely casual character. To this point we will shortly return.

Ponds in which rare Rotifera have been found once, have been under regular observation for years; these rare pond forms may in some months totally disappear; in others year after year they always seem to be rare. To these very species belong all those badly described males, of which the naturalist has only had the good fortune to get a "glimpse", but not material enough for a more thorough study. And even with regard to these species it certainly happens that exhaustive studies in nature itself will now and then fall in a locality, where such a rare species really has a great maximum with succeeding sexual periods and occurrence of males and resting eggs. Elaborate studies year after year in the same locality and at the same time and the same temperature will then very often result in the failure to find the phenomenon again later on; the colony now year after year propagates only parthenogenetically with abated propagation in winter and with a little quicker propagation in the summer half-year. — This is f. i. the case with the *Triphylus* colonies, in North Sealand.

With regard to the fixed Rotifer societies, those composed of the families *Meliceridae* and *Flosculariidae*, it might at a first glance seem difficult to speak of maxima at all. More thorough investigations from recent years have shown that this is really allowable. *Lacinularia socialis* as well as different *Melicerta*-species may, mainly at the highest summer temperatures, develop real carpets, with which they coat the substratum upon which they are fastened. I shall return to this point in the second part of this work.

As soon as a maximum for a given species is observed in nature, the time has arrived when it may be taken into the laboratory. Owing to the enormous amount of specimens, pure cultures are easily procured. In very many cases the males then appear in the cultures in the very week in which the material was taken in from nature. The life time of these cultures is commonly very short, often only a few days, but the time is long enough to procure the males. In the winter half-year, when no sexual period occurs, they may live for months.

If we will try to found cultures from a few specimens of the same species and at other times of the year, as far as my experience goes, it is quite impossible to produce a maximum or a sexual period. Most probably, this is only possible for the Rotifera of the pools that are drying out. At all events all these Rotifera, which have been used for experimental work in the laboratory, and in which it has been possible to develop sexual periods experimentally, belong to this category. It must however be emphasised, that the researches, now published, have not been combined with more thorough experimental work. It would be of the greatest interest if this was one day carried out upon Rotifera belonging to localities which do not dry out. In the winter half-year I have often had different species of *Brachionidae*, *Eu-*

*chlanidae*, *Anuraeadae*, in my aquaria. I have here never seen a trace of a sexual period. In the summer half-year the cultures of all these species have always died out in the course of a few weeks, during the sexual periods in the course of a few days.

The investigations in nature have further shown that very many of those Rotifers which are really very common pond Rotifers belonging to the vegetation zone and occurring in almost every pond f. i. *Dinocharis pocillum*, *Cathypna luna*, *Monostyla cornuta*, many of the *Philodinidae*, *Pterodina patina*, *Metopidia* and many others, hardly ever occur in those great maxima which are characteristic of many plancton Rotifers, or for such species which are living in pools that are drying out (f. i. *Hyalina senta*). They are common the whole year round, perhaps a little more common in summer than in winter, but all in all, great variation in number the whole year round cannot be demonstrated. Even in these pond species, the males are either totally unknown or only observed once in a single specimen. If however these very pond Rotifers are studied year after year and in very many localities, it happens, as stated above, that the naturalist now and then comes across ponds, where now one now another of the above-named specimens occurs in countless numbers, i. e. has one of its great maxima. I have seen these great maxima in several of the *Philodinidae*, *Pterodina patina*, *Metopidia lepadella*, *Monostyla cornuta*, but only a few times in the course of twenty years and only in a single locality. Commonly these great maxima occurred in the winter half-year. They were enormous immediately before the ponds were frozen; they were observed under the ice during the first weeks, but when the ponds thawed in April, they had disappeared again. These species were cultivated in the laboratory during the maxima, the localities were visited at intervals of only a few days, the results were always the same: not the slightest sign of sexual periods: neither males nor resting eggs. Nevertheless the observation is by no means without scientific value; more thorough investigations may perhaps really find the males in other localities and fix the sexual periods. There is f. i. no doubt that very many of the *Philodinidae* have their greatest maxima in the winter below the ice; if a sexual period should exist in this family too, and the males most probable occur only sporadically and only at great intervals in the life history of a colony, it is most probable that this would especially take place during the winter half-year.

It may besides be emphasised, that it is very dangerous to conclude from the failure to discover the sexual periods in a species (demonstration of resting eggs and males), that this does not exist. Firstly it must be remembered that even if a species in a given locality or a given latitude usually only propagates parthenogenetically, in other localities and other latitudes males may occur and sexual periods set in. This seems f. i. to be the rule with regard to many Ostracoda, the males of which seem to be wholly absent already in our country, whereas they appear in Bohemia and are common in Algeria.

Experience further shows that even for the very same pond, in which the investigations are carried on, it is dangerous, on failing to ascertain a sexual period,

to conjecture that the species in this locality only propagates parthenogenetically. For many years this investigation totally lacked the males of very many genera, even such in which the males were described by earlier authors. Maxima were observed, sexual periods, however, not.

In 1920—22 a rather extensive investigation relating to the study of the sexual propagation in *Oligochaeta* was planned. It was shown that the *Oligochaeta*, in those periods when the sexual products were to ripen, were in search of those algæ-carpets which cover the surface of small ponds like scum, especially at the highest summer temperatures. It was further shown that the tp. in these algæ carpets might in spring rise to about twenty-eight degrees celsius, even if the tp. a few inches below the surface was only about 18—20 C. Undoubtedly the worms used the extremely high temperatures to ripen the sexual products; very many of our *Oligochaeta* hitherto regarded as rare f. i. *Vejdowskyella*, *Pristina*, *Slavina*, *Ripistes* were found here, and almost all were found in the sexual period, this being for many of the species either totally unknown, or at all events only observed rarely. The investigation, carried on by one of my assistants Mag. LAKJER, whose death was a great loss to my laboratory, induced a wish on my part to see whether the Rotifera did not also use the algæ carpets in the same way as the *Oligochaeta*. My idea was correct, and it was shown that in the very same ponds, in which I had for years been in search of Rotifer males, belonging to species which were extremely common here in the female sex, and of which, nevertheless, I never saw any of the males, the latter could be procured as soon as the algæ carpets were peeled off from the surface by means of glassplates. These algæ carpets acted as a substratum upon the underside of which very many creeping Rotifers, at other times of the year living in the littoral or upon the bottom of the pond, were to be found in great numbers in the sexual period. Almost all the Rotifera which passed their sexual periods on the undersurface of the algæ carpets, belonged to the creeping or slowly swimming species. Just these species hardly ever carry their eggs; they were deposited upon the underside of the carpets and owing to the high temperatures ripened there in the course of very few hours.

On the algæ carpets in various pitholes, on the same moor, different Rotifers would simultaneously show great maxima; in seven pitholes on the same moor I simultaneously found maxima of *Salpina mucronata*, *Melopidia triptera*, *Euchlanis dilatata*, *Triphylus lacustris*, *Copeus labiatus*, *Dinocharis pocillum*, *Scaridium longicaudum*.

Commonly every little pithole had almost pure cultures of the different species; a more thorough investigation further showed that the different species succeeded each other in the hole; in one pithole great maxima of *Euchlanis dilatata*, *Dinocharis pocillum*, *Scaridium longicaudum* and *Triphylus lacustris* succeeded each other serially. The algæ carpets came on the surface in the middle of May at an airtp. of about 18—20° C., they were used by the *Oligochaeta* and Rotifera (most probably also by some *Copepoda*, especially *Harpacticidae*, and *Ostracoda*), till the first part of July; then very high summer temperatures set in, and the tp. in the algæ carpets reached



28—30° C. Then almost suddenly the rich microscopical life in the carpets disappeared. Quite the same result was gained the next year, when heavy and incessant showers filled the pitholes and diluted the water. The algæ carpets did not disappear, but during the rest of the year, they were not, or only very rarely, used.

During the stay of the animals upon the carpets, the underside was used as a locality in which the eggs were laid. As well known, the male eggs are commonly smaller than the female eggs; simultaneously with the hatching of the eggmasses on the algæ carpets in the vessels, we tried to find male eggs, and if possible isolate them. The investigation showed, that just in these species, the difference in the size of the two sorts of eggs is really but small, and that with regard to the length of the diameter they overlap each other.

Many of these pond Rotifers have been studied at regular very short intervals in the very same ponds from the moment they appeared on the algæ carpets and to the moment they again disappeared — the period commonly lasted three or four weeks —; fresh material was brought to the laboratory every second or third day. Often great maxima were developed before the eyes of the observer; great quantities of eggs were deposited in the vessels. The main task was to procure the males, and in many cases the task was really accomplished. There is no doubt, that if it had not been observed that these carpets were used as localities in which the eggs were deposited, most of the males belonging to the creeping or slowly swimming Rotifers would not have been found.

I am inclined to suppose that the investigation, in the manner in which it is carried on, is more likely to give an idea of the occurrence of the males under natural conditions than previous investigations. The common impression is that the males among these Rotifers from perennial ponds are extremely rare. Huge maxima may really set in, the ponds may teem with females, but the females are almost all female producers, only very few male producers occur. When the specimens are hatched in the vessels, most of them seek the lighted edge of the vessels; hour after hour the edges are sucked clean by a pipette and the material brought under the microscope; among many hundreds of females belonging to specimens of the common pond rotifer life, one or two males appeared; during the whole period the number was not augmented. Often the vessels have teemed with *Dinocharis*, *Triphylus*, *Stephanops*, *Scaridium*, species of *Diurella*, *Metopidia*, *Cathypna*, *Monostyla*, *Rattulus*, *Notommata* but of most of the species, even if they were studied in freshly gathered material, collected at intervals of only a few days, it was impossible to get a single male. Of some of the species f. i. *Dinocharis* and *Scaridium longicaudum* WEBER observed the males in Switzerland. What especially favours the supposition that a sexual period really does not appear in our latitudes, at all events not in all localities, and not every year, is the circumstance that of these species it has almost always been impossible to get the resting eggs. Just upon this point there is the greatest difference between the species from perennial ponds and those from pools drying out, where the males are regularly found. The algæ carpets, upon which *Hydatina* colonies have

laid their eggs, are often after the sexual periods so to speak dark spotted with resting eggs.

Only for some of the Rotifers from perennial ponds f. i. *Triphylus lacustris*, *Asplanchnopus myrmeleo* did the resting eggs appear and clearly showed that the males, in spite of the utmost care, had escaped observation. In connection with this fact, it must be remembered that just because so very many of these Rotifers in my area of investigation developed their maxima simultaneously, it was necessary in the very same weeks, in the time from about 15 May to 15 June, to work at the highest pressure possible. What could not be managed in this time, could not be carried out before the next year. When that year arrived, fresh investigations were carried out upon those Rotifers in which the males had escaped my attention then, but it often happened that, in these very localities, just these species did not appear that year. In this way, it happened that the males of *Eosphora digitata*, *Triphylus lacustris*, several *Notommatidae* and others could not be procured.

That the males of all these Rotifers from perennial ponds are able to escape the investigation is due not only to their presumed rarity, but also to several other facts. Even if they are in some degree attracted by the light, this is not so much the case as with the plancton Rotifers; all the specimens do not seek the lighted edges of the vessels, very many of them never leave the algæ coatings upon which they are born, and which cover the whole surface of the vessel, this makes it much more difficult to find the males of these species than of the plancton Rotifers, of which both sexes immediately dart towards the light source. Rotifers from out-drying ponds especially *Hydatina senta* are only in a very slight degree attracted by light.

Another factor which makes it difficult to find the males of very many pond Rotifers is that the males in many of them are almost of the same structure as the females; they are certainly smaller but not smaller than young newly born females. Whereas a male of a plancton Rotifer, owing to its extremely small size, its peculiar shape, and the enormous speed with which it moves, is easily recognised, the slowly moving males of many of the pond Rotifers, shaped like young females, are very difficult to interpret for what they really are; much time is therefore wasted in bringing presumed males, which are really only young females, under high power.

If however it is correct that many of these pond Rotifers attain huge maxima, without any sexual period as the result, the question is, how this presumed fact may be understood. — I am here inclined to suppose that, in all species, the huge maxima inaugurate a sexual period, but that external factors, climatic conditions, prevent its further development. The investigation has shown that, owing to sudden heat, and especially owing to sudden and very heavy rain, the large maxima may almost immediately be arrested. It seems, as if a strong and sudden dilution of the water is able to kill the specimens in the course of very few hours; the eggs which these specimens have laid, are then developed, but the external conditions, under which this new brood is to live, do not allow of the rapid development of the sexual products which is the condition of the development of the great maxima.

Even if many maxima seem to be arrested without any pronounced sexual period, a closer study of the colony will show that a sexual period has really been intended. In the sexual periods the ovary commonly gets darker, and often changes its colour from yellow to blue; this change in colour characteristic of impregnated male producers may take place in a colony almost simultaneously in very many of the females and rather suddenly, often in the course of only a few days.

Almost simultaneously with the change of colour, the males appear; in a few cases I have, during large maxima seen this alteration in colour of the ovaria; then the maxima were suddenly brought to cessation, and no resting eggs were observed.

A more thorough investigation will perhaps further show that we may also in other ways calculate beforehand when the sexual periods will occur. Even if this must be mainly regarded as music of the future some few observations seem already now to make the following worth mentioning.

MAUPAS and later on especially American authors have made it highly probable that, at all events in *Hydatina senta*, we possess two sorts of females, the female producers and the male producers; the first-named produce only eggs from which females appear, the others eggs which, when unfertilised, give rise to males, when fertilised, to resting eggs. In how far these observations may be brought to bear upon all Rotifera, we do not know. For the present we only know, that in outer form and in general anatomical structure the two sorts of females cannot be distinguished from each other. — There is however the possibility, that more thorough investigations will find out these differences and furthermore, that they will perhaps prove much more conspicuous in other species than in *Hydatina*. — For several of the plancton Rotifers it may often be shown that the specimens which carry the small male eggs, are of a smaller size than those which carry the fewer and much larger female eggs. This may be even more conspicuously observed in *Polyarthra platyptera*, where the male producers are often only half the size of the female producers, and have a much more pointed form. Already HUDSON-GOSSE have observed this; in Tab. XIII fig. 5, 5 b the two sorts of females are clearly figured. As however the females that carry the resting eggs, are larger than those that carry the male eggs, and have not the peculiar acuminate form, it is probable that the acumination of the body in the male egg carrying females, is only a juvenile character which is obliterated during growth. In some ponds I have seen *Triarthra mystacina* suddenly disappear at the moment when the male producers appeared, and be replaced by *T. longiseta*, which at that time was male egg carrying.

As I have never been able to keep *T. longiseta* in the aquaria for more than a few days, I have not been able to pursue the observations more thoroughly.

At all events, after we have learned that the female sex in the Rotifera is most probably divided into two forms: female and male producers, it is a natural course to enquire, whether there might not, here as in the case of the Aphids, possibly be some difference in the outer form of the two sorts of females, and all the more so



since, of several species, we know rather peculiar varieties, which almost in all localities where the species occur, appear rather suddenly and then disappear again. How much stress we are able to lay upon that point is however questionable as some of these varieties carry as well male eggs as female eggs. This is the case f. i. with *Polyarthra platyptera* var. *euryptera*. Already ROUSSELET (1896 p. 265 Tab. XI. fig. 2) has shown this.

With regard to the modes I have used to study the structure of the males, the following information may be given. As the males of almost all the species are extremely small, it was very difficult to isolate them. Most of them have only a size of about 100  $\mu$ ; many only 40—50  $\mu$ . Males which are more than  $\frac{1}{2}$  mm. may be regarded as veritable giants and occur mainly among the *Asplanchnade*, and some genera of *Notommátide*. The isolation was done by extremely fine pipettes, by means of which they, after having been detected under a Seibert Microscope lense Obj. 0 Oc. 0, were sucked up and brought under a Zeiss Microscope. The drop of water was then made as small as possible, and a cover laid directly upon the drop, no waxfeet were used. Commonly there was sufficient water under the cover for the free swimming motion of the male; owing to slow evaporation of the water, the time arrived when the male was found to modify its motions; asphyxia owing to diminution of the amount of oxygen or to the accumulation of carbonic acid caused the animal to lie in the same spot, motionless, but with the wheel-organ wholly stretched out and with the cilia moving in the water. In this situation the animal could live from thirty to sixty minutes and in this time it was studied and drawn. Commonly there were in the vessels many or very many males of most of the species; if so, male after male was used. The animals were lying without any motion at all, and it was possible to draw them with Abbes camera. The lenses which were used, were almost always homogen immersion Apochrom. 2 mm. and Comp. Oc. 6, if necessary also the excellent Orthoscopical ocular, which with hom. im. gave the power of 1500 times. A strong electric lamp was almost always necessary. The greatest difficulty was to watch the male under low power, often for hours, until that moment arrived when the animal had ceased to move.

When studying the male under hom. immersion, it could further be shown that, when the time arrived when the strength of the animal was almost exhausted and the cover slowly pressed it more and more, the different organs appeared, one after one, with increasing clearness; this was due to the stronger and stronger compression of the hypodermal layer.

All drawings are made by means of Abbes camera; as however the males did not live for more than an hour, and often many males were used, many drawings of the same males were worked out, whereupon all the drawings were combined into one single one; commonly the outer contour of a male was given from one specimen, and the anatomical details from another or very often from a whole series of males.

Narcotic fluids and staining fluids have only been used for the largest males,

especially those of *Asplanchna*. Narcotising fluids may really help to keep the animals more steady; on the other hand they die faster; then the results were only very badly preserved wheel organs, with the cilia without any regularity straddling in all directions; fixation and staining methods have only been used for the largest males (*Asplanchna* and *Hydatina*) but even here I do not think that the result corresponded to the labour. More than a general anatomical description the methods, employed by me, are not able to give; the histology of the animals cannot be studied in this way. Owing to the exceedingly small size of the animals, and the great difficulties connected with procuring sufficient material, this investigation will be extremely difficult. When I have restricted the investigation strictly to the anatomical description, it is because I am of opinion that the more elaborate histological investigations, as well as many others, do not belong to the series of researches which should be carried out at the freshwater biological stations but in a much higher degree have their natural home in the laboratories, belonging to the great universities. According to my experience it is impossible for a single person to carry out an investigation such as this, in all its different phases. What is gained, is here as always, only a step up the ladder of our knowledge; others, with other abilities and another training, may then try to take the next step.

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## Chapter II.

### Systematical Remarks.

With regard to my views concerning the systematic position of the Rotifera and their mutual relationship, I will not here enter too much into details. Already in 1899 I tried in a paper published in Danish to reform the system of HUDSON-GOSSE, which in my opinion is only in a very slight degree the natural expression of the mutual relationship of the families. It has been a great satisfaction to me to see, that DE BEAUCHAMP, (1909) whose paper inaugurates a new era in our knowledge of these most interesting animals, is in accordance with my view upon many essential points. Published in Danish, my paper has suffered the fate of being misunderstood or not understood at all, especially in the chapters relating to the wheelorgan and mouthparts. As far as I have been able to see, the points of agreements between DE BEAUCHAMP's and my results are more numerous than DE BEAUCHAMP seems to think. The system was further adopted by HLAVA (1908), and v. HOFSTEN (1909). Now, about twenty five years later, I am quite aware that the system, even if upon some points perhaps it was an advance, upon others, suffered from considerable errors. DE BEAUCHAMP has tried to correct these errors; owing to insuf-

ficient knowledge of those genera, which DE BEAUCHAMP maintains are placed very incorrectly and used by me as intermediate stages between forms which according to his idea have nothing to do with each other, I do not wish here to enter too much into details. I hope later on to be able to show that on some of the points where our views do not coincide, my arrangement is not so "fantastic" as DE BEAUCHAMP seems to think.

Here I only take the liberty to give a short summary of the results at which I arrived in 1899, and which I am unable to alter upon essential points. It is upon these results that my systematic views, which I shall finally set forth in a few words, are based.

The cuticula of the Rotifera is originally segmented; the lorica, which arises owing to coalescence of the middle segments, and in which the anterior and posterior segments may be drawn in, is a derivation of the hyaline segmented cuticula.

The original wheel-organ of the Rotifera is a ventrally placed ciliacovered disc, without any specially developed wreath of cilia, bordering the disc; the mouth lies excentrically in the hindpart of the disc. Animals, equipped with wheel-organs of this type, are slowly creeping; the swimming power is extremely small, and the motion, in swimming, is along a straight line, not rotating. The wheel-organ is unable to procure food during the swimming motion.

The more a type of the Rotifera is emancipated from the substratum, passing over from a creeping to a swimming organism, the more terminally is the ciliacovered disc placed, and the more will the cilia, bordering the disc, be equipped as a ciliary wreath; simultaneously with this, the cilia coating of the disc will diminish, and finally the disc will be almost or totally nude. The locomotion passes over from straight to screwformed; the number of rotations is dependent on how much the ciliary wreath is developed in relation to the cilia of the disc. In the most aberrant types of the wheel-organ, it is further modified in such a way, that it is able to capture food during the swimming motion. In accordance with this the disc is often first cleft in two half, between which the mouth is placed; then a new wreath of cilia will be developed, either inside or outside the primary ciliary wreath; the main purpose of this second wreath is to prevent the organisms, caught by the primary wreath, from escaping and to carry them safely to the mouth opening. In accordance with this, a furrow, bordered by the two ciliary wreaths, the locomotory wreath and the stopping wreath, is developed; through this furrow the nourishment is carried to the mouth by means of cilia.

I arrived at this main result with regard to the wheel-organ, more from the study of the manner in which the animals used the organ, than from an anatomical investigation. With low powers, equipped with a small microscope, often in nature itself, I studied the animals in open vessels; later on I only used a very strong lens, observing the animals in high cylindrical vessels. From his anatomical studies, as far as I can see without a more thorough study of the freeswimming organisms, DE BEAUCHAMP (in 1907 and later on in 1909) arrived at a result, which in its



main lines may be said to be almost congruent with mine. On many essential points he has elucidated the facts, given my suppositions a solid basis, and corrected some of my views that were undoubtedly wrong. On the other hand, having for years studied the wheel-organs with his elaborate studies in mind, I feel convinced, that the want of observations of the freeswimming animals has on some points been unfortunate for his views, just as the want of a more thorough anatomical examination has been unfortunate for my views.

I have referred the wheel-organs to six different types, of these the first, *Nottommatidæ*, the fifth the *Melicertidæ*, *Pedalionidæ* etc. the fourth (*Hydatinidæ*, *Brachionidæ*, *Anuræadæ*) have many points of contact with those of DE BEAUCHAMP. My type No. 2 comprising the *Dinocharidæ*, *Coluridæ*, *Rattulidæ*, *Salpinadæ*, *Cathypnadæ*, *Euchlanidæ*, *Ploesomatidæ*) are by DE BEAUCHAMP referred to his type No. 4. This is perhaps more correct, the primitive form *Cyrtonia*, which is of great significance for the understanding of this group, being unknown to me. My type No. 3 comprising the *Synchaetadæ* and *Asplanchnadæ* is the most erroneous; here the study of the wheel-organ of *Eosphora*, which was also unknown to me, has shown how the wheel-organ of the *Asplanchnadæ* is to be interpreted, and that that of the *Synchaetadæ* is better connected with his type No. 4. My type No. 6, the wheel-organ of the *Floscularidæ* DE BEAUCHAMP also refers to a special type; his attempt to connect it with that of the *Melicertidæ* is in my opinion a great mistake.

One of the greatest merits of DE BEAUCHAMP is his excellent studies of the retrocerebral organ; just the clear indications of the openings for this organ has made it possible for him to establish his excellent scheme of the general type of the wheel-organ, and find the homologies in the different special types. I am inclined to think that, if my work had been written in another language, it would be manifest that by my mode of investigation I have through observation and reasoning arrived at many of those mainpoints in the anatomy of the wheel-organ in the Rotifera which were only fully scientifically elucidated through DE BEAUCHAMP's researches.

Simultaneously with the wheel-organ undergoing very considerable modifications the mouthparts are also modified. Originally the mouthparts play a prominent part in the procurement of food; in accordance herewith they are shaped as prehensile organs, by means of which the food is seized and carried into the mouth. The more the wheel-organ is modified to catch the food, the more too they are altered to be only a masticatory organ. Only in the freeswimming families *Asplanchnadæ* and *Synchaetadæ*, where the wheel-organ is only a locomotory organ, the mouthparts are prehensile or clasping organs. There is really the most conspicuous conformity between the different types of wheel-organs and mouthparts. These last named organs may be referred to two main types, the malleate and the forcipate, those of the mainly detritus and planteaters and those of the typical animals of prey. Both types are to be found in the primitive forms. The more the wheel-organ during the forming of the secondary wreath of cilia is able to procure food for the animal, the more the significance of the mouth parts as prehensile organs is diminished (the malleate

mouth parts of the *Brachionidae*), and where the wheel-organ is finally transformed in such a way that a real canal for the food between the two wreaths is performed, this function is totally lost. In accordance with the fact that the mouthparts are unable to procure food and be forced out into the mouth opening, they are more and more withdrawn from it. A beginning of the transformation already takes place in types with malleoramate mouthparts, but is fully developed in the *Philodinidae* and *Floscularidae*. They have here, especially in the *Philodinidae*, lost all significance as prehensile organs, and placed in the middle of the body, they only play a rôle as triturating masticatory organs.

In the creeping Rotifera the foot is an organ of locomotion and fixation; in the swimming Rotifera, it is mainly a steering organ; it is reduced or often totally lost in most of the real planctonorganisms. As the foot is highly variable and modified in accordance with the main functions it has to fulfil, systematical characters can only in a very slight degree be gathered from this organ.

The Rotifera possess two pairs of almost conform sensitive organs, which may be designated as the anterior and posterior lateral organs; whereas the posterior preserve their original position, this is not the case with the anterior organs, which as a rule meet each other dorsally in the middle line and here coalesce to an unpaired sensitive organ of different form; for this organ the name dorsal organ is often used. Only rarely, f. i. in the *Asplanchnadae* and in *Apsilus*, they have their primitive position, lying separated laterally before the posterior lateral organs.

The light preserving organs are one median, commonly larger unpaired eyespot, below the brain, and two paired spots, placed before this, and often in a special part of the ciliary disc. Only rarely all the three eyespots are present, commonly only the unpaired one, more rarely the paired one. With regard to the retrocerebral organ the reader is referred to the excellent studies of DE BEAUCHAMP, who was the first to show that this very peculiar organ is typical of very many, and most probably of all, the Rotifer-families. It is most strongly developed in the more primitive families of the Rotifera, and strongly reduced in the typical plancton Rotifera and in the fixed families.

The nerve system has only been very little studied, thoroughly only in a very few species; it is of interest that everywhere where more thorough investigations have been carried out, these studies have ascertained the presence of suboesophageal as well as pedal ganglia.

The excretory organs are of almost quite the same structure in the whole group, and present no characters which may be used for the systematical arrangement of the different families. On the other hand, perhaps just this organ, more than any other, clearly shows the systematical position of the whole group in the animal kingdom.

With regard to the muscle system it may be pointed out, that in this quite especially, as well as in the cuticula, and in the arrangement of the lateral organs, in the more primitive forms we find certain rather conspicuous indications of

a segmentation in the organisation, which on one side cannot be quite overlooked, but upon which, on the other side, not too much stress must be laid.

It now will be understood that I regard the soft indistinctly segmented cuticula as more primitive than an unsegmented lorica, the ventral ciliary disc as the primary wheel-organ from which the wheel-organ with two ciliary wreaths has been developed, the foot which is not sharply defined from the remaining body and provided with two toes as the most primitive footform of the Rotifera; further that I regard the dorsal organ as developed from coalescence of two originally separated lateral organs. As I further call attention to the fact that the great reduction in the structure of the males is most feebly pronounced in the *Notommatidae*, it will be understood that I regard this family, in which all the above-named primitive body structures are more or less distinctly developed, as the most primitive of all the families of the Rotifera. A closer study will show that just this family possesses the developmental possibilities of the plurality of the other families, and that remarkably many of the Rotifer-families, through more or less conspicuous transitional stages, seem more connected with this family than with each other mutually. It seems as if most of the other families of Rotifera may be arranged in a series of parallel developmental lines, all deriving from the *Notommatidae*; some of the lines may be drawn with almost full certainty; with others this is not the case; some, showing no connection at all, seem to be totally aberrant forms.

In my opinion the Rotifera were originally creeping organisms, bound to the bottom and the vegetation. Secondly in different ways their organisation has been altered in such a way, that from creeping organisms they have been changed into freeswimming creatures, more or less independent of the substratum, in the aberrant forms true plancton organisms. These processes of modification by means of which it is only possible to understand many of the most peculiar body-structures, (the connection between distinct types of mouthparts and of the wheel-organ, the structure of the foot, the development of the lorica, the loss of segmentation, the peculiar balloon shape, manifesting itself in very different genera (*Asplanchna*, *Synchaeta*, *Notops* (*N. pelagicus* Jennings) have begun not from a single but from different *Notommatidae*, the results of which are series of different developmental lines running parallel. The *Notommatidae*, themselves, are almost all creeping or very slowly swimming organisms. Only one plancton organism (*Proalidies* DE BEAUCHAMP 1917 p. 148) is known.

In 1899, when this view was published, even if some of the main points had already been observed by previous authors (METCHNIKOW 1866 p. 354; JOLIET 1883 p. 204) the system, set forth by HUDSON-GOSSE (Vol II p. 14), was the dominating one. Upon all essential points their views differed totally from mine. According to them the *Notommatidae* were the most highly developed family of all the Rotifera; the typical wheel-organ was two ciliary wreaths (*cingulum* and *trochus*). Great stress was laid upon the fact whether a lorica was present or not. Characters deriving from homogeneous life conditions were used as characters which connected families together in the same order, and which had no affinities at all. The old interpreta-



tion deriving from BURMEISTER and LEYDIG and still maintained by HUDSON-GOSSE, that the Rotifera were Arthropoda, either related to Crustacea or Insects, caused *Pedalion*, when found, to be referred to a special order, showing special affinity to the Arthropoda (v. DADAY 1886 p. 214). In all essential points the system was adopted by PLATE (1891 p. 320) who only introduced the apparent and commonly adopted improvement: The removal of the *Philodinidae* and *Seisonacea* as *Digononta* in contradiction to all other Rotifera (*Monogononta*). Especially after CLAUS (1895 p. 1) and LEVANDER (1894 p. 32) had shown that *Pedalion* had no Artropod characters at all, the old supposition, that the Rotifera showed affinity to the Arthropoda, was abandoned, but nevertheless the systematical arrangement of HUDSON-GOSSE was still preserved and mainly used in Deutschlands Süßwasserfauna (1912) as well as in WEBER's (1898) and MONTET's (1918) treatment of the Rotifera in Switzerland. A great improvement was made by HARTOG (1910 p. 220) who separated the Rhizota into two orders, *Flosculariacea* and *Meliceracea*, otherwise the system of HUDSON-GOSSE was preserved rather unaltered. This rather persistent adherence to this system, was mainly due to the fact that the Rotifera, almost simultaneously with their happily escaping affinity whith the Arthropoda, owing to a superficial resemblance between some Rotifera, especially the *Trochosphaera* just detected at that time and the *Trochophora* larva, were regarded either as forerunners of the Annelida (SEMPER 1872 p. 305, HATSCHKE 1878 p. 100 a. o.) or as larvæ of Annelida which have arrived at maturity, neotenic Annelidalarvæ (LANG 1888 p. 186). It will be clearly understood that this view can only be adopted when the typical wheel-organ is regarded as two ciliary wreaths, corresponding with those found in the *Trochophora* larva and must be totally abandoned, if the ventrally placed, cilia-covered disc is regarded as the typical one. As mentioned, already in 1899 I found the comparison with the *Trochophora* larva and the attempt to connect the Rotifera with the Annelida to be a total mistake, almost just as great as the attempt to connect them with the Arthropoda. The Rotifera are nearly connected with the Turbellaria, in which I am inclined to see their nearest allies. As far as I understand, this is also mainly the opinion af DE BEAUCHAMP (1900 p. 56), who especially seems to lay stress upon the *Gastrotrica* as the connecting link between the two groups.

Before entering upon the description of the males I think it most reasonable to give a short sketch of my views on the relationship between the families. My systematical views, set forth in 1899, have been criticised by DE BEAUCHAMP who, even if he is in accordance with me on many points, in many others differs considerably from me. DE BEAUCHAMP has summarised his criticism in the following sentence "Il (W-L) a pressenté les vrais rapports dans les cas, ou il les a énoncée, plutôt qu'il ne les a démontrés". This remark, is indeed quite correct. As it may most probably be used as a motto over almost all my papers, as well as over all zoological work, carried on in Nature herself and performed upon the basis of thoughts and ideas which have arisen during the excursions themselves, more from

the study of the living organisms, than from that of the organisms in hardened and stained condition, I embrace the opportunity to offer the following remarks.

DE BEAUCHAMP and I have quite independently of each other in opposite ways tried to reach the same goals, a more correct understanding of the position of the Rotifera in the animal kingdom and of the systematical relationship between the families. In DE BEAUCHAMP'S work the centre of gravity unquestionably lies in the laboratory work, in mine it is in Nature herself. The way which I have been forced to follow, is determined by personal inclination and by my scientific position as the leader of a biological laboratory situated in the midst of Nature far removed from the large centres of culture. May I here insert the following remarks.

The establishment of biological stations was, based upon the clear understanding of the fact that in the long run the practice of carrying out zoological and botanical studies to a greater and greater extent in large laboratories, situated in the large towns, far away from living Nature was connected with great danger. When it has so often been urged that so many of these laboratories, especially the freshwater biological laboratories, have not yielded the expected scientific results, this, apart from many other causes, is also due to the fact, that they have not sufficiently marked out the limits of their investigations, aiming sometimes too low and sometimes too high. What has been lacking is the cooperation between the two kinds of laboratories; what has augmented the difficulties of cooperation is on the one side the, certainly not always unfounded, want of respect for the studies from the freshwater biological laboratories combined with too great a confidence in the exactness of the scientific methods used in the town laboratories, and on the other side a lack of power from the freshwater biological laboratories to carry out their investigations in Nature herself, and an often rather unfortunate need to prepare and accomplish the investigations in ways which only in a very slight degree differ from those which the great laboratories in the towns are forced to follow.

Laboratory investigations, especially those relating to the biology, but partly also those relating to the anatomy of animals, very often give one the impression of being somewhat accidental both in regard to their plan and their results. The reason for this must probably be sought in the fact that the observer unconsciously works with the individual as an isolated element. He has great difficulty in maintaining a clear perception of the organism as a link of a whole, transformed, and influenced by the circumstances under which it lives, and in turn exercising a similar influence on its surroundings. Laboratory studies may at any rate lead to results, which dazzle by a seemingly far greater accuracy than that which it is, as a rule, possible to attain through studies in nature. It must, however, be borne in mind, that these so-called accurate results are arrived at by methods of research, which have their strength especially in their one-sidedness, but on account of this, they have also hidden in them all the sources of erroneous inferences, which necessarily arise from all one-sided researches. For my own part I am very often in doubt as to how far this "accuracy" in many cases is anything more than an illusion, and

whether the results arrived at in nature, with due consideration to its endless and manifold qualities, have not on the whole, as great a scientific value, even if the results in question appear in a more unostentatious, and less dazzling form.

The investigations which are commenced and rest upon profound studies in Nature and the results of which are later on subjected to thorough investigations in the laboratories, are those which most promote science.

As far as I am able to see DE BEAUCHAMP agrees with me in the following main points: We have both arrived at the result, that the *Turbellaria* may be regarded as the nearest allies of the Rotifera; that the primitive wheel-organ of the Rotifera is a ciliary disc, placed ventrally and encircled by long cilia; that the system of HUDSON-GOSSE must upon all essential points be regarded as very unnatural. With regard to the order *Scirtopoda* DE BEAUCHAMP confesses that HUDSON-GOSSE "exagérait l'importance" of *Pedalion*. The division of the Ploïmes in *Loricata* and *Illoricata* is "nefaste". In contradiction to HUDSON-GOSSE but in accordance with my views DE BEAUCHAMP regards the *Notommatidæ* as the most primitive of the families; upon my "groupement des familles en séries divergentes à partir des *Notommatidæ*" he says that it has "peu de changements à subir et se retrouve en bonne partie dans le tableau ci-contre (p. 41)".

On the other hand we disagree upon very essential points, and it is easy to show that this is due to the different mode in which we have studied the great questions in which we have both been interested.

The three main points are the following: (1) The systematical position of the Rotifera; (2) the different use we make of our criticism of the system HUDSON-GOSSE, and (3) the systematical arrangement of some of the families.

1. Even if DE BEAUCHAMP is like myself inclined to see in the *Turbellaria* the nearest allies of the Rotifera, he also believes he can find affinities with the *Gephyrea*, the *Brachiopoda*, the *Axobranchia* and quite especially with the *Mollusca*. I shall not here enter into detail with regard to the discussion of the affinities with these groups, but only pay attention to one point which I think has hitherto been rather overlooked.

In contradiction almost to all other great divisions of the animal kingdom which are bound to fresh water, the fresh waters seem to be the real home of the Rotifera, the element in which the group originated. What characterizes the freshwater fauna is, that it is an emigrant fauna, either deriving from the sea or from the land, a fauna of emigrants, the home of which was originally to be found everywhere, not only in the element in which it lives nowadays, i. e. in the freshwater itself. Owing to the peculiar conservatory power of the freshwater with regard to all types of animals which, from the oldest epochs of the earth and to our own day, escape into it, the freshwater fauna is a relict fauna, to which the oldest prehistoric oceans, as well as our present ones have provided and still provide their contingents. We are not for a moment in doubt that the developmental centres, with regard to *Bryozoa*, *Spongia*, *Crustacea*, *Coelentera*, *Insecta*, *Mollusca*, *Fishes*, have never lain in the fresh-



waters; what occurs of these great divisions in freshwater, is only to be regarded as remnants, separated from the main stock, often in the dawn of the earth. As far as I have been able to see, the Rotifera is the only division of freshwater organisms which cannot be regarded from this point of view. It seems as if their developmental centre has really been in the freshwaters: they are almost lacking in the sea, and apart from the very aberrant *Seisonacea*, they never develop special forms there. That the land Rotifera, the moss fauna of the trees, derive from freshwater, needs no further explanation. Owing to this view, which is allowable, especially with regard to animals about whose Phylogeni Palæontology gives no answers at all, I am disinclined to see near relationship with marine animals.

The view given above is further strengthened by the following fact. If we look over the other freshwater organisms with marine derivation, it is easy to show that the members of these different divisions, the *Spongia*, the *Bryozoa*, the *Coelenterata*, the *Crustacea*, the *Fishes*, are a remarkably casual medley of organisms, the affinities of which are often either much nearer to marine organisms than to freshwater organisms belonging to the same division of animals, and with which they live side by side. At the present time they very often show no affinities at all with organisms from this very geological epoch, whereas their affinities with extinct marine animals are regarded as established facts. However different the Rotifera may be, this view cannot be shared with regard to them: just this very peculiar phenomenon, that so very many of the families of the Rotifera may be arranged in developmental lines with their extreme stages finishing in plancton organisms, and with their starting points traced back to creeping organisms, gives support to the idea that they have a common source.

That further all these developmental lines really originated in freshwater and not in the sea, is in my opinion obvious, because during their development they adapted themselves biologically in accordance with those rules which many other freshwater organisms have been forced to follow, if exactly this element, the freshwater of the earth, was to be used as a home for these organisms. I am here thinking especially of the propagation, the heterogoni, the great rôle the resting eggs play in the life of the Rotifera, the absence of larva stages, all phenomena which the Rotifera share with so many other freshwater organisms, and which can only be pointed out in a very slight degree or not at all in the marine fauna. That the reduction of the male sex may be partly observed from the same point of view, I shall try to show later on.

If the above-named supposition, that the freshwater is the native home of the Rotifera is correct, and if further it is correct that the creeping, slowly swimming bottom and littoral forms are the most primitive forms, the *Turbellaria* must be regarded as those freshwater organisms from which we are best able to trace the derivation of the Rotifera. Simultaneously it will be understood that I am only with difficulty able to share the views of DE BEAUCHAMP, according to which the Rotifera should be more or less related to a great number of marine animals. My view is especially based upon the structure of the excretory organs, common to both divi-

sions, and on the view of the wheel-organ advanced above. And it is at all events not weakened by the fact that, with regard to the biology of the animals, especially with regard to the propagation in the Freshwater-Turbellaria, we find all those phenomena again in greater or smaller degree, which govern the propagation of the Rotifera (heterogoni, parthenogenetic propagation, resting eggs, no larval stages) whereas in the marine Planaria, if present at all, they must be regarded as great exceptions (see v. GRAFF 1882, p. 145). During recent years several authors especially GROBBEN in his "Lehrbuch" and partly MARTINI (1912, p. 627) have tried by means of the Gastrotricha to connect the Rotifera with the Nematoda. As far as I can see, the structure of the excretory organ and that of the Nematoda present great difficulties for this arrangement.

As well known, most of the authors before me have maintained, that the developmental centre of the Rotifera should be looked for in the freshwaters and not in the sea. This is the case with HUDSON (1889, p. 437), DADAY (1892, p. 95), LIE PETERSEN (1905, p. 1), DE BEAUCHAMP (1909, p. 59), v. HOFSTEN (1912, p. 163). Only ZELINKA (1907, p. 1) has maintained quite the opposite view, asserting that the developmental centre should be looked for in the sea. He has been opposed especially by DE BEAUCHAMP, and mainly by quite the same arguments as I would have used. It is not necessary to go into details upon this point; I refer the reader to the above-named papers, especially those of DE BEAUCHAMP and of v. HOFSTEN. I only wish to add that the authors, as far as I have been able to see, with regard to their conception of the systematical position of the Rotifera have not drawn the consistent conclusion from their interpretation of the original home of the Rotifera.

2. It has been pointed out that upon many essential points DE BEAUCHAMP and myself agree in our criticism of the system of HUDSON-GOSSE. Whereas I draw the inference of the criticism and, working upon it, try to reform the system, DE BEAUCHAMP returns to the system of the English authors saying: "le vieux groupement en ordres emprunté à DUJARDIN et à HUDSON demeure le meilleure avec les corrections que nous avons faits" (p. 40). As however the conception of the *Notommatidae* as the most primitive of all Rotifer families, the arrangement of the other families in developmental lines deriving from them, and the interpretation of the division of Ploima into Lorica and Illoicata as "nefaste", so to speak totally subverts the whole system of HUDSON-GOSSE, I cannot see that it is scientifically defensible to return to it. When DE BEAUCHAMP says about my system: "Son groupement en ordres et sous-ordres est beaucoup plus contestable" (p. 39) than my arrangement of developmental lines, deriving from the *Notommatidae*, I fully agree with him. I only take the liberty to add that the system of HUDSON-GOSSE cannot be regarded as better for that reason. When DE BEAUCHAMP is able to return to this system while I am not, this is due to the different starting points of our investigations. He who has based his investigations of the Rotifera upon studies in Nature, and understood how the developmental lines, starting from the creeping animals and ending in the plancton organisms, have slowly been developed, and further seen how the organisation has

been altered in accordance with variation in life conditions, will never be able, because of his investigations, to return to this system. I only wish to add that even if I have been forced to attack the system of the learned English authors, my admiration for what these two Scientists have done to promote science in this difficult domain of natural history, has in no way been abated. It will always be the work to which all students of this group of animals will return; in my opinion this is mainly due to the excellent and exact contour drawings of the animals, which only rarely give room for doubts with regard to the conception of the animals which the authors have described.

3. With regard to my arrangement of the Rotifera in developmental lines, starting from the *Notommatidae*, it is with the greatest interest I have seen that DE BEAUCHAMP has arrived at quite the same result for some of them. This especially holds good for the line *Notommatidae*. *Hydatina*, *Notops brachionus*. *Brachionus* and *Anurea*.

I suppose that it is quite correct, as DE BEAUCHAMP has done, to separate the *Ploesomatidae* from the next line, consisting of *Triphylus*, *Harringia*, *Asplanchnopus* and *Asplanchna*. Nearly related to it, is the small developmental line of *Notops hyptopus*. *Ploesoma*. *Gastropus* and perhaps *Anapus*, a line which begins in the *Notommatidae*, especially with forms related to *Copeus*.

The *Synchaetidae* which are taken by both of us with quite the same restrictions, are in my opinion nothing but *Notommatidae* that have emancipated themselves from a substratum; they are closely associated with the *Notommatidae* through such species as *N. aurita* and *N. pilarius*. Researches from recent years show that the last stages in this developmental series show structures very similar to those which we find in the genus *Asplanchna* (balloonshape, peculiar humps etc.). See especially PLATE (1889, p. 1), LEVANDER (1895, p. 21), ROUSSELET (1909, p. 170).

The lines comprising the old loricate families *Rattulidae*, *Diaschizidae*, *Euchlanidae*, *Coluridae*. *Dinocharidae* and *Cathypnidae* cannot be drawn with such great certainty as the above-named; in the *Notommatidae*-*Rattulidae* and in the *Notommatidae*, *Diaschiza*, *Salpina*, *Euchlanidae* I see two different developmental lines. The genera may perhaps be arranged in a somewhat different way, and the families *Coluridae*, *Dinocharidae* and *Cathypnidae* placed in this great division. All in all this does not obviate the greater difficulties of the systematic view which is advanced here, and DE BEAUCHAMP's arrangement may most probably be said to come as near to the truth as possible; great differences between his results and mine do not seem to exist.

Upon all these points there is no doubt that DE BEAUCHAMP has given my views upon the systematical arrangement of the Rotifera that scientific basis which they most certainly lacked, and upon many points he has introduced improvements. Some of the most aberrant families, the *Trochosphaeridae* and *Seisonacea*, are still without any systematical connection with the other Rotifera, and for my own part I am doubtful as to whether the *Seisonacea* may be referred to the Rotifera at all.

With regard to the *Bdelloida* DE BEAUCHAMP is in doubt as well as myself as to whether the placing of them and the *Seisonacea* in a special division, *Digononta*, in



contradistinction to all other Rotifera is really correct (PLATE). Along quite different roads we have arrived at the same results, he starting from the wheel-organ of *Adineta* and I especially from the behaviour of the creeping *Diglena*. In the present state of our knowledge I suppose it is impossible to come nearer to the truth than DE BEAUCHAMP gives it (1909, p. 36). "On ne s'aurait donner les Notommatides comme ancêtres aux Bdelloïdes, mais le rapprochement nous éclaire beaucoup, plus même que celui de ZELINKA avec *Rhinops*, d'ailleurs soutenable avec les mêmes réserves, sur la morphologie de l'extrémité céphalique des Philodinidés." *Adineta* as well as *Microdina paradoxa* show structures which further seem to strengthen this view.

Because of insufficient knowledge with regard to the dorsal organ and lateral organs and in consequence of the presumed want of a contractile vesicle PLATE (1887, p. 258) has been inclined to see in the *Pterodinidæ* a family which was related to the *Philodinidæ*. Owing to great resemblances in the mouth parts (malleo-ramate and ramate) and in the wheel-organ, I confess I have shared this view. As however ROUSSELET (1898, p. 24) has shown that a dorsal antenna is present, that the lateral antennæ are only placed further forward than in most of the other Rotifers, and has further pointed out the existence of a contractile vesicle, I admit that this view cannot be maintained. As further he has described the very peculiar *Brachionus pterodinoides* from Devil's Lake, North Dakota (1913, p. 59), which really seems to be related to the *Pterodinidæ*, it is perhaps most correct to refer this family nearer to the *Brachionidæ*.

With regard to the *Rhizota*, DE BEAUCHAMP and I take quite different views, and upon this point I cannot alter the systematical arrangement set forth in 1899. The order *Rhizota* is only established owing to the common stamp which, everywhere in the animal kingdom, and quite especially among fixed animals, common modes of life set upon the organisms. The characters of the order given by HUDSON-GOSSE are: "Fixed when adult, usually inhabiting a gelatinous tube, excreted from the skin: foot transversely wrinkled, not retracted within the body, ending in an adhesive disc or cup" (1889, p. 43). Later authors (COLLINS, WEBER) have certainly expanded the description of the order, but as far as I can see, they have not augmented the characters which should justify its establishment. If the description of HUDSON-GOSSE is altered a little with regard to the sentence "foot transversely wrinkled", it will be seen that it may be used as a characteristic of many groups of fixed animals (f. i. fixed Infusoria), and it will be understood that all these characters are wholly adaptive. The *Rhizota* contain species with the most different wheel-organs, one wreath of cilia, two wreaths of cilia, no wreath at all; the greatest possible differences in the structure and form of the coronal disc; the placing of the cilia and their structure. The mouthparts are malleate, malleo-ramate, and uncinatæ; the buccal orifice placed centrally and ventrally; the anus ventrally, terminally or dorsally, often situated high up upon the dorsal side, the rest of the alimentary canal of the most different structure. In the arrangement and structure of the lateral organs the differences are also great.

Already DUJARDIN but more especially HARTOG (1910, p. 220) understood this. The last-named author referred the two families, the *Flosculariadae* and the *Meliceridae*, to two different orders *Flosculariacea* and *Meliceracea*. DE BEAUCHAMP (1909, p. 32) again refers them to the order *Rhizota*, comprising the two suborders *Meliceriens* and *Flosculariens*. HLAVA (1904, p. 25) has divided the *Meliceridae* into two subfamilies *Meliceriens* and *Conochiloidiens* and DE BEAUCHAMP (1908, p. 129) refers them to two different families *Meliceridae* and *Conochiloidae*. Later on DE BEAUCHAMP (1912, p. 242), in accordance with the work of Miss FOULKE, (1884, p. 37) divides the *Flosculariens* into two families, the one comprising the three genera *Acyclus*, *Cupelopagis* (= *Apsilus*) and *Atrochus*, the other the genera *Floscularia* and *Stephanoceros*. The order *Rhizota* is then according to DE BEAUCHAMP divided into two suborders *Meliceriens* and *Flosculariens*, each with the above-named two families. With regard to the standpoint of HARTOG and myself he further adds: "Il ne faut pas exagérer, comme l'a fait W.-L., jusqu'à nier tout rapport entre ces deux groups et leur en attribuer de très artificiels avec d'autres." (p. 32) In my opinion there is not the slightest affinity between the two great families, each of them is much more closely related to various freeswimming Rotifera than to each other, and as long as this is not clearly understood, these very families cannot be systematically placed.

Owing to the structure of the mouth parts, the wheel-organ, the form of the body, the peculiar "limbs" (*Triarthra brachiata* ROUSSELET 1901, p. 143. Pl. VIII, fig. 7.) *Triarthra* and *Pedalion* may be referred to the same family, *Pedalionidae*. This was done by me in 1899 and so far DE BEAUCHAMP shares my views. A close examination will further show great mutual congruity upon all essential points between the *Meliceridae*, and *Pedalionidae* (mouth parts, wheel-organ with two ciliary wreaths). In my opinion *Pedalion* is a pelagic Melicerid which has preserved the wheel-organ and the mouth parts of the *Meliceridae*; the changed mode of life as a freeswimming organism has caused the loss of the foot and the peculiarly shaped "limbs". How the two peculiar stylate ciliated appendages in *Pedalion* are to be interpreted, I do not know.

To see adaptive features due to common life conditions in all these common characters is quite impossible, the one family being fixed, the other consisting of freeswimming plancton organisms. DE BEAUCHAMP (1909, p. 29) says: "Par ce double caractère (malleoramate mouth parts and two ciliary wreaths) on a voulu les rapprocher des Rhizotes Meliceriens, qui les possèdent également. J'ai montré que la convergence due à un même mode d'alimentation suffisait à les expliquer." His views have been set forth at greater length already in 1908 (p. 128). Upon this point I quite disagree with the learned author; of course the mode of nourishment is the same in the two families; but whence does this mode arrive, which is common to them both and which, being once elaborated in this form, is unique among the families of the Rotifera.

Which seems the more natural to suppose, that the combination of malleoramate mouth parts and the two ciliary wreaths showing in all their details the greatest

conformity in the two families *Meliceridæ* and *Pedalionidæ*, have been developed independently of each other in fixed as well as in freeswimming organisms, or to conjecture, that this unique combination, used under very different life conditions, suggests affinity between the two families. Most probably the wheel-organ in the *Meliceridæ* is the best for procuring detritus food, on the other hand it is rather weak as a swimming organ, the result of this being the development of the jerking thorns and limbs which are more developed in the *Pedalionidæ* than in any other family. The thorns are used to alter the direction, which these footless species would otherwise have been unable to do. In my opinion the *Meliceridæ* and *Pedalionidæ* may be placed in the same division; to connect this with the *Notommatidæ* is at the present time impossible.

When DE BEAUCHAMP claims that he has "montré" (1909, p. 29) that convergence due to the same mode of nourishment enables us to demonstrate the conformity between the two families *Meliceridæ* and *Flosculariadæ* I confess that, from my standpoint, I can only see that, in these domains of investigation, whether our researches are carried on in Nature or in the laboratories, we can never get any further than to "enoncer", never to "montrer" anything (vide pag. 40).

The *Flosculariadæ* in my opinion form a rather heterogeneous group; as I however have never had an opportunity to see *Apsilus* and only on a journey a glimpse of *Stephanoceros*, my views are of no value. I have thought that *Microcodon* was in some way related to the *Flosculariaceæ*. WEBER seems to have been of the same opinion (1888, p. 18). DE BEAUCHAMP maintains, that its wheel-organ "se rattache facilement à celui de *Cyrtonia* par l'intermediaire du genre voisin *Microcodides*." I hope to return to this point later on.

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## Chapter III.

### The Males of the Rotifera.

#### Fam. *Notommatidæ*.

As mentioned before I regard the fam. *Notommatidæ* as the most primitive of all the families from which most, perhaps all, of the other families may be derived. I regard it as quite impossible to indicate more thoroughly the closer relationship between the many genera of *Notommatidæ*. In the following I draw upon the work of MAX VOIGT (1912, p. 82).

Nowadays very few males of the fam. *Notommatidæ* are known. The males of the genera *Albertia*, *Drilophagus*, *Pleurotrocha*, *Theorus*, *Taphrocampa*, *Monommata*, *Arthroglena*, *Distemma*, *Triopthalmus*, *Otoglena* are all quite unknown; for a few of them now one, now another, author has stated that he has seen "a glimpse of a male", but this of course is of no scientific value.

Only the males of the genera *Cyrtonia*, *Proales*, *Diglena*, *Copeus*, *Notommata* and



*Triphylus* have been described and figured; those of *Cyrtonia*, *Triphylus* and *Notomata* only a single time and very insufficiently. On the other side WEBER's descriptions of *Diglena catellina*, *Diglena forcipata* and *Copeus labiatus* and further ROTHERT's and ROUSSELET's descriptions of *Proales Wernecki* belong to the best descriptions hitherto known of males of Rotifers.

### *Cyrtonia tuba* (Ehrbg.)

Male: Rousselet 1894 p. 433.

ROUSSELET (1894, p. 433. Pl. XX, fig. 4) describes the male as follows.

The male of *Cyrtonia tuba* is a small elongated, cone-shaped creature with only a slight indication of being humped, and otherwise quite straight, having a simple ciliary wreath, a prominent red eye, dorsal and lateral antennæ, a contractile vesicle and two small toes. The jaws and alimentary canal are quite absent, the elongated sperm sac filling the whole body cavity. The usual longitudinal muscular bands, which are striated, are present, and the circular bands are more apparent than is generally the case. The two small toes are conical and have the usual foot glands. Size of female  $\frac{1}{10}$  inch to  $\frac{1}{100}$  inch; of male  $\frac{1}{250}$ . Time: June—August.



*Cyrtonia tuba*  
♂ (Ehrbg.)  
after Rousselet.

### *Proales Wernecki* Ehrbg.

Male: Rotherth 1896 p. 702.

Rousselet 1897 d p. 415.

In 1896 ROTHERT described the male but gave no drawing of it; next year ROUSSELET found the male again and gave a new description and two figures. In the following I have tried to combine the two descriptions.



*Proales Wernecki*  
♂ Ehrbg. after  
Rousselet.

The male is of much the same appearance as the female; this especially holds good with regard to the form of the body, foot and wheel-organ. It differs from almost all other male rotifers in having a well-developed alimentary canal. It has a mastax of a structure almost quite like the female. The jaws are like those of the female. All the usual parts are well developed, and, in addition, there is a small triangular plate on each side articulated between the ramus and uncus. There is a well-defined oesophagus and small salivary glands. The stomach is also present, but takes up a very small portion of the body cavity; an intestine cannot be seen. The gastric glands are only small, much smaller than those of the female. There is a large testis but no prostata gland; the spermsac opens as usual into a penis on the back of the foot. The brain and the red eye correspond with those of the female. The excretory organ is only insufficiently observed; there seems to be no contractile vesicle. The toes and foot glands are large. A dorsal antenna but no lateral antennæ are observed.

The males are found swimming in the water; in form and structure they are very like the young females but differ strongly from the old, stout, almost globular females found in the galls. Size of male  $149\mu$ , of young female  $159\mu$ , of adult female  $195\mu$ . Time: according to Rotherth, December, according to Rousselet, April.

The young female when first hatched is of much the same size and appearance as the male; but the large, white, rounded, salivary glands attached by a narrow neck to the mastax, and the large and full gastric glands, as well as the ovary and stomach, which together fill up the whole body cavity, serve to distinguish it at once. Both the young male and female escape from the galls in which they have been hatched by an opening which is formed at the apex. They swim about in the open water for a time, whereupon the young female again enters a *Vaucheria* filament, but where and by what means is not exactly known. It causes the plant to produce a rounded or elongated gall of considerable size; it seems that the female is unable to develop and lay eggs outside the *Vaucheria* filament or gall. The adult female is almost globular with a large number of immature eggs. Most probably intestine and stomach are active. Some galls contain all female eggs, others both female eggs and the smaller and fewer male eggs. Fertilised resting eggs were found by ROTHERT in a number of 30–54 in one gall, all laid by a single female.

### *Proales parasita* Ehrbg.

Tab. I, fig. 4–6. Tab. IX, fig. 7–12.

**Description:** Body cylindric, very short. Wheel-organ placed almost vertically, consisting of a row of cilia; upon the disc a horse-shoe shaped second row with somewhat longer cilia. (Tab. I, Fig. 6). Brain very large; dorsal antenna most probably present, but has not been observed; lateral antennæ not observed; a very large red eye placed behind the brain; no trace of alimentary canal. Testis very large, pearshaped, opening dorsally; no penis but the ductus seminalis can be turned inside out; at the opening a tuft of cilia. Two prostata glands. No trace of excretory organs. A real foot does not exist, but there is a peculiar sharply defined small appendix, ending in two spinelike projections. There are six or seven transversal muscle bands and two pairs of longitudinal ones. The interior is filled with a greyish mass, containing very many oil globules. Size of male 40  $\mu$ , of female 160  $\mu$ .

It is only with some doubt that I refer this species to *Proales parasita*. This as far as I know has hitherto only been found in *Volvox*, in which I have often found the animals too. My specimens all derive from *Uroglena volvox*. Owing to the smaller size of this alga the animals do not always live in the colonies; very often they sit on the outside, feeding upon the surface. Often they jump off, swimming round the colonies. The eggs are laid upon them. When newly hatched, the females are small, narrow and rather quick in their movements; but in the course of a few days, after having fed upon the *Uroglenas* they begin to swell; the foot with the toes is almost always held withdrawn, and at last the whole body is quite deformed. (Tab. I, fig. 7–12). In this shape the animals hardly ever leave the colonies, often living within them and almost filling them up. When *Uroglena* colonies are not at hand, the animals live their life as freeswimming organisms, and the females keep the shape indicated in fig. 8. The females possess no tentacle in the wheel-organ and cannot therefore be identified with *Hertwigia volvocicola* Plate. As I cannot find any difference between the *Proales parasita* Ehrbg. and my specimens, deriving from the *Uroglena* colonies, I refer them to this species. In my area of exploration it is common in May.

### **Hertwigia volvocicola** Plate.

Male: Plate 1886 p. 27.

PLATE describes the male as follows. (1886 p. 27).

Die Männchen fanden sich nicht eben selten, meist in 3—4 Zahl, innerhalb der Gallerte der Volvoxkugel. Sie sind walzenförmig und haben eine Grösse von nur 0.08, übertreffen daher die Hälfte der Länge des Weibchens um ein Weniges. Sie sind sehr einfach gebaut und entbehren der Mundöffnung, des Kauapparates und eines besonderen Penis. Der Räderapparat besteht aus einem Cilienkranze, der die Mitte der Bauchseite freilässt und über den die Cuticula sich etwas hervorwölbt zu einer dichte mit kleinen Wimpern besetzten Calotte. Besonders bemerkenswerth ist das Fehlen des kegelförmigen Hautzapfens, welcher den Kopf des Weibchens überragt. Der Leibessaum wird vornehmlich von dem Hoden erfüllt, dessen flimmernder Ausführgang am hinteren, etwas verjüngten Körperend, ausmündet. Das Gehirn stellt ein im Verhältniss zur Körpergrösse enorm entwickeltes Organ dar, dem am Hinterrande ein roter Augenfleck ansitzt. Mit Sicherheit habe ich nur einen dorsalen Taster bemerkt, doch ist der andere wohl übersehen worden. Über dem Hoden liegt der rudimentäre Darm, der vorn bis an das Gehirn reicht und mit diesem so eng zusammenhängt, dass ich oft einige Körnchen des Augenpigmentes auf ihn übergetreten fand. Die Wassergefässe sind vorhanden, doch nur sehr schwierig zu erkennen, sodass mir die Art ihrer Ausmündung verborgen blieb. Nur dass ist sicher, dass eine contractile Blase fehlt. In dem rudimentären Darm habe ich nie Spuren von Kalkkörperchen, wohl aber zuweilen einige Fetttropfen gefunden. Das Hinter- und Vorderende des Körpers können etwas eingestülpt werden.

### **Notommata naias** Ehrbg.

Male: Rousselet 1903 p. 176.

Wesché 1902 p. 327.

Tab. I, fig. 1—2.

ROUSSELET says that he has described the male of *Notommata naias*. I have not hitherto been able to find the description. WESCHÉ (1902, p. 327 Pl. XVII, fig. 2 a b) has described the male as follows:

The general shape is fusiform, with a slight tendency to angularity. The head is well separated from the body, which is long in proportion to its breadth and distinctly annulated. The foot is long with four annulations. The toes are identical with those of the female, each furnished with a big gland which extends into the body some distance beyond the orifice of the penis. The cilia are moderately long, with several indistinct setæ. The brain is large, and retracted by two powerful bifurcate muscles. The eye is very large, dark red, standing out from the brain (as in ♀), and there is a slight constriction where it joins the brain. The dorsal antenna seemed placed very much forward on the brain, but was not distinct. The lateral antennæ were quite clear, and on the lower part of the body. Below the brain was a granular mass, and adjoining were some nebulous glands, which seem to be the remains of the digestive organs. The vascular system was distinct, but no contractile vesicle could be seen. The spermatheca was very large, extending well into the middle of the body. Size 212  $\mu$ . Time January, March.

**Description.** Body elongate, truncated in front, attenuated behind, foot long thick, three jointed, not sharply defined from the other part of the body. Two short toes. The whole body very soft, flexible, altering in form, covered by a very soft hyaline cuticula; at the attachment of the transversal muscles regularly constricted



and with regular longitudinal folds which are especially conspicuous on the foot. Wheel-organ a slanting cilia-covered disc, surrounded by a wreath of somewhat longer cilia and with a broad bunch of long cilia on the top; no visible auricles.

No mastax; as a remnant of the alimentary canal a longitudinal folded sac-like body lying over the testis and fastened by ligaments to the body wall. Brain large with a broad red eye; a dorsal antenna with a bunch of short bristles; no lateral antennæ have been observed. Four longitudinal muscles. Very conspicuous are six transversal muscle bands which regularly contract and expand the body; during swimming and creeping this is always altering its form. The two lateral canals carry each three vibratile tags; no contractile vesicle visible. A very large pyriform testis with two sorts of spermatozoa; a long ductus seminalis covered with cilia; penis short ending dorsally upon the second foot segment; cilia coating round the opening; two short foot glands. —

The descriptions of WESCHÉ and myself do not agree very well but as there is also considerable discrepancy between his drawings and his description a comparison is difficult.

Size of male 120  $\mu$ , of female 300—400  $\mu$ . Time: April. Several times I have met with this slowly swimming or creeping animal. It appeared rather often in cultures which contained only *N. naias*; the very thick foot and no, or at all events very small, auricles are both characters which the male shares with the female.

### **Notommata aurita (Müll.)**

Tab. I, fig. 3.

**Description.** Body subcylindric, ventricose, furnished behind with a short tail, by no means so conspicuous as in the female. Cuticula thin, extremely flexible, altering in form with a peculiar, rather constant system of longitudinal lines dorsally; the course of these lines will best be understood from the figure. Foot short with two joints, well separated from the body; two rather short acute toes. Wheel-organ a cilia-covered slanting disc of triangular form, surrounded by a wreath of rather short cilia. Seen dorsally the wheel-organ presents itself as bent inward; there are two well-developed auricles. Alimentary canal absent; as rudiment above the testis a rather inconspicuous sac or band. Brain very large, broad, with a large flattened eye, a conspicuous dorsal antenna lying remarkably near the wheel-organ. Of the retrocerebral organ a very conspicuous opaque part containing a large number of concretions; further two subcerebral organs which I have not been able to see in so conspicuous a position that I have ventured to draw them; they are concealed between the six large cells of hypodermal nature and are indicated in the figure. That they really exist, is so much the more probable, as shortly before the death of the single specimen I have seen, I with certainty observed two rounded openings which most probably are the openings of the organ. The lateral antennæ I have not been able to see. Two lateral canals with three vibratile tags each, but no contractile vesicle.

Three pair of longitudinal muscles for the wheel-organ and one pair acting as a retractor for the foot. Testis very large, globular, with two kinds of spermatozoa; a thick ductus seminalis covered with cilia; genital opening upon the first foot segment; the opening surrounded by a wreath of cilia. Two prostata glands; above the testis a globular mass of opaque concretions. Two small foot glands. Size of male 180  $\mu$ ; of female 250—330  $\mu$ . Time July.

***Diglena forcipata*. Ehrbg.**

Male: Weber 1897 p. 94. 1898 p. 487 Pl. XIX fig. 8.

WEBER (1897 p. 94 Pl. IV, fig. 2) has described and figured the male.

It is of almost the same form as the female and also almost of the same size. It terminates in two long toes, widely spread and separated at their base by means of a little probosciform tubercle. As in the female the body is covered with a rather thick, hyaline cuticle, representing a sort of lorica; this is restricted to the dorsal side and ending a little below the forepart of the body; behind it reaches the base of the foot. The head is curved downwards and the coating with cilia reaches the niveau of the mastax. The forepart of the body carries two strong transversal folds, the one passing over the dorsal antenna, the other passing over the end of the brain. The foot is thick, the footglands are well developed, pyriform. The wheel-organ is a large, ventral plate, covered with cilia, concave. Four longitudinal anterior, two longitudinal posterior and five transversal muscles, forming regular folds in the skin. No probosciform tubercle at the front of the head as in the female. No trace of alimentary canal. Two excretory canals each carrying three vibratile tags open upon each side of the penis. The brain is oblong with two frontal eyes. A brilliant point above the brain is observed; whether this is a dorsal antenna is doubtful. The testis is relatively small; the penis is terminated by a crown of small stiff cilia. Prostata glands are not observed but yolkmasses above the testis.

***Diglena grandis* Ehrbg.**

Tab. I, fig. 7.

**Description.** The male has almost quite the same form as the female and is but little smaller. It is cylindrical, tapering behind and also a little in front. Cuticula extremely thin and hyaline, provided with a system of regular longitudinal folds. It is thickest dorsally and in the middlepart of the body; forepart and foot can partly be drawn into the middlepart. No chitinous arched plate as in the female. The body terminates in two long acute toes. Brain large; it gives off a nerve for the dorsal antenna; lateral antennæ I have not been able to observe. Two red eyes placed very near each other. Wheel-organ a large disc, placed almost vertically to the longitudinal axis, highest in the middle and drawn out dorsally and ventrally in small auricles. It is surrounded by a wreath of long cilia. No particular styli observed. Of the alimentary canal there is only present the connecting band between testis and wheel organ. The two lateral canals carry three or four pairs of vibratile tags; there is no contractile vesicle. Testis pear-shaped large; ductus seminalis without cilia. Opening for the copulatory organ at the posterior border of the last foot segment. The co-

pulatory organ consists of a chitinous sheath which may be regarded as a continuation of the envelopment of the testis. The sheath consists of two hyaline chitinous bands, separated from each other; between them is the real penis, which is a little shorter than the sheath. The penis can be protruded and then the whole body will be curved often in such a high degree, that it is almost ball-shaped. There are two prostata glands. Above the testis is a globular mass, containing many opaque corns of irregular, often quadrangular, form. At all events there are three or four transversal muscle bands, most probably more, and four strong pairs of longitudinal muscles. Oil globules wanting. Two foot glands. Size of male  $300\mu$  of female  $300-350\mu$ .

The species was common in a little pond near Hellebæk, North Seeland (Time  $14/V$  22); it was easily recognisable from almost all other *Diglenas* only by means of its size. The pond was covered by a peculiar carpet of waterplants mainly formed by *Myriophyllum* and *Lemna polyrrhiza*. When squeezing this material in a plancton net, very many different Rotifers appeared. Among them one of the most characteristic was this large, extremely voracious animal, which preyed upon all that came near it. Isolated in the vessels many eggs were laid upon algæthreads and a few males appeared in the light-illuminated border of the vessel.

#### ***Diglena catellina* Ehrbg.**

Male: Weber. 1888 p. 46.

— 1898 p. 494. Pl. XIX fig. 13.

Tab. I, fig. 8.

WEBER (1888 p. 46; Pl. XXXIV fig. 1, 4, 5) describes the male as follows.

Body cylindrical, differing in form from that of the female, a little smaller, more stretched, narrower and slightly curved on the dorsum. Cuticula very thin and hyaline. The wheel-organ exactly in accordance with that of the female; a feeble groove where the mouth is to be found in the female. A well-developed muscular system which has not been more thoroughly studied. The digestive system totally absent; in its place a long series of granulations. Vascular system consisting in two canals, beginning near the brain and opening on each side of the penis; the opening round, encircled by cilia; only three vibratile tags seen; in the female four. No contractile vesicle; an olive-formed brain with a dorsal antenna. Two eyes on the forepart of the head. The foot with long; slender, acute toes. Testis piriform, very large, suspended by means of fine ligaments from the bodywall and by means of a muscle to the wheel-organ. Near the base a longitudinal striation, probably deriving from muscles. Penis covered by a cuticula, it is very different from those hitherto described in Rotifera. WEBER describes it as follows: »A la base du testicule et y faisant suite, nous voyons chez *D. catellina* un organe en forme de navette, formé de deux bandes aplaties, concaves à l'intérieur et convexes à l'extérieur, se réunissant et se terminant en pointe à l'extrémité postérieure du pénis. Les deux bandes chitineuses sont la continuation de l'enveloppe du testicule; elles sont dures, séparées l'un de l'autre par un espace dans lequel se trouve le pénis. Cette enveloppe chitineuse protège le pénis délicat et sert à forcer le cloaque de la femelle. C'est un étui protecteur, droit, long et étroit. Le pénis lui-même est fort mince et cylindrique; son orifice n'atteint pas l'extrémité de l'étui, qui est ouvert, fendu dans toute sa longueur. Autour de cette gaine cornée du pénis, nous voyons une gaine musculaire en fourreau et des muscles rétracteurs de cet



ensemble que j'appelle l'organe copulateur. Le pénis est placé sur la face dorsale du pied. Lorsqu'il est complètement retiré son extrémité arrive juste à la racine des doigts du pied et est protégée par deux petits bourrelets circulaires. Au même niveau, de chaque côté, débouchent les canaux latéraux du système excréteur.»

**Description.** Male of almost the same form as the female, but in front almost cylindrical, only tapering behind. It is more elongate, narrower than the female, but curved on the dorsum like this sex. The cuticula is very thin, hyaline and extremely flexible, it is thickest dorsally and in the middle part of the body; the forepart can be withdrawn, the posterior part only in slighter degree. The wheel-organ formed exactly like that of the female; some stronger hairs on two elevations on the disc. No frontal hood. The brain is large, perhaps not always faintly bilobed behind, and with a nerve to the dorsal antenna; no lateral antennæ have been observed. Two red eyes as in the female. Of the alimentary canal only a connecting band between the testis and wheel-organ; WEBER regards this band as being of muscular substance. The excretory organ consisting of two canals with three vibratile tags; no contractile vesicle; WEBER has seen the opening of the canals on both sides of the penis; I have failed to see them. Testis large pyriform, suspended by means of fine ligaments. The copulatory organ formed as in *Diglena grandis* and in close accordance with the admirable description of WEBER. Two very small prostata glands. Above the testis a globular mass. Four transversal muscle bands; four pairs of longitudinal bands and at all events one pair of slanting muscles from the base of the foot to the dorsal antenna. Two foot glands. No oil globules. Size of the male 140  $\mu$  of the female 150  $\mu$ .

*Diglena catellina* is here as everywhere an extremely common animal. In May it was found in the algæ carpets almost in every pond; and many eggs were laid in parts of these carpets which were brought into the vessels. The males were rather common, though always rarer than the females.

### ***Diglena giraffa*. Gosse.**

Tab. I, fig. 9.

**Description.** Male extraordinarily slender, tapering posteriorly, straight, of an almost incredible hyalinity, flexible in a degree which has perhaps never been observed and moving with an enormous speed. I never succeeded in making camera drawings of it, but I got some measures when the animal was fully stretched out, and could study the internal structure rather exactly. The form differs very much from that of the female, having no marked neck and no tumid abdominal part, the whole body being almost hairshaped, only a little thicker in front than behind; the toes are very long, straight, the cuticle is soft, without any longitudinal folds, the whole animal bluish hyaline almost quite invisible. The wheel-organ as in the female, but without any frontal hood, insufficiently observed. Brain pearshaped with nerves for the dorsal organ; two red eyes placed very near each other. Of the alimentary canal only a band. Lateral canals with three vibratile tags; no contractile vesicle.

A large strongly elongated testis; owing to the extreme slenderness of the body a copulatory organ could not be observed; only a long ductus seminalis but not covered with cilia; a bunch of cilia at the opening of the penis on the posterior border of the last segment. No prostata glands observed. Six transversal muscle bands and at all events three longitudinal muscles. Two pedal glands. No oil globules. Length of male 250—280, but measured without pressure most probably only 15—20  $\mu$  broad. Length of female 250—280  $\mu$ .

It is only with some hesitation, that I have determined this species as *D. giraffa* Gosse. It was found in great quantities in a little pond, near Hellebæk, North Sealand (Time  $12\frac{1}{2}$  22). The female was characterized by a well marked neck and a very tumid abdomen; a frontal hood, two red eyes and two long slender straight toes; it was in full accordance with the figure by HUDSON-GOSSE (Pl. XIX, fig. 9). It was extremely restless and variable in form. It lived in the alga coverings on the surface of the pond; a little of this material was isolated with many hundred specimens; two days later the males appeared; it was only by means of the greatest accuracy and with the best possible light conditions that it was possible to detect the males which, with regard to restlessness, hyalinity and especially slenderness, surpassed all that has hitherto been observed. The eggs were laid on the carpets, resting eggs were not observed.

#### ***Diglena mustela* Milne.**

Male: Milne 1885 p. 188.

According to Hudson-Gosse Suppl. p. 31, MILNE has described the male: "It is a much smaller animal than the female, more elongated, and with a more developed hood. Its structure is normal." I have not been able to get MILNE's paper.

#### ***Diglena volvocicola* Zawadovsky.**

Male: Zawadovsky 1916 p. 1.

ZAWADOVSKY (1916 p. 1) has described and figured a *Diglena* from *V. globator*; he describes the male, gives some figures of the pairing process and mentions that some minutes after having been hatched the males are ready to copulate. The paper is written in Russian with a very short resumé.

General remarks. The *Diglena* males are characterized by being shaped almost like the females; they are only more slender than these; there does not seem to be any neck; they only taper posteriorly not in front and there is no frontal hood. They are extremely hyaline without any lorica, but the skin is thicker in the middle part of the body and thickest on the dorsal side; commonly the foot is not sharply defined. The species described have all the wheel-organ formed like that of the female, but it has a more vertical not a ventral position. The two eyes are visible; only the dorsal antenna has been observed; no mastax and only feeble rudiments of the alimentary canal; no contractile vesicle; vibratile tags fewer in number than in the female; most probably the lateral canals always open on the side of the

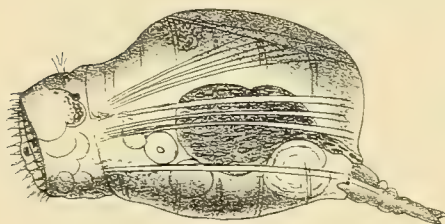
penis at the posterior border of the last segment. The testis is pyriform and the copulatory organ has probably always a rather complicated structure; with regard to this point I refer the reader to WEBER's description. Remains of yolk almost always present. Two foot glands and no oil globules.

The *Diglena* males have hitherto only been observed by WEBER. For a long time I vainly searched for them. Not till 1920, when I learnt that, in the sexual period, the eggs were laid in the algæ carpets on the surface of ponds, was I able to detect the males of three species. The males which always seem to be much rarer than the females, are only met with in May; they are creeping like the females but swimming too and with much greater speed than the females; the motion is always straight; no rotating motion has been observed. I have never seen the pairing process, so well described by Weber for *D. catellina*.

### ***Triphylus lacustris* Ehrbg.**

Male: Western: 1892 p. 374.

WESTERN (1892 p. 374. Pl. XXV fig. 5) has observed the male but only once and has only given a very insufficient description and figure of it. He only says:



*Triphylus lacustris* ♂. Ehrbg. after Western.

"The digestive viscera are entirely wanting; their space is occupied by the large sperm sac. A large penis protruded behind the foot was observed. The males were found swimming amongst females. Length  $\frac{1}{88}$ ."

The first time I met with this peculiar rotifer was in May 1898 in a little pond near Furesø. It was very common, but I missed the sexual period. The pond was then almost filled with dead leaves, branches etc., and I could never find the species again.

In later years I have often seen the animal and have visited the ponds where it was common at regular intervals. In summer as well as in winter I found females with resting eggs, but curiously enough I never succeeded in finding the males.

### ***Eosphora digitata* Ehrbg.**

Male: De Beauchamp 1905 p. CCXXX.

DE BEAUCHAMP describes the male as follows.

"Le male d'*E. digitata* est remarquable par sa dégradation beaucoup moins grande qu'elle n'est habituelle chez les Rotifères; sa forme générale est absolument celle de la femelle et sa taille n'est pas beaucoup inférieure ( $310 \mu$  contre 415 en moyenne); son aspect est tout à fait celui d'une jeune femelle, d'autant plus qu'il a conservé les amas de granulations de part et d'autre de l'œil qu'elle possède à ce degré de développement. Couronne, cerveau, pied et ses glandes, muscles, vessie sont exactement semblables; sur les canaux excréteurs je n'ai pu compter que trois flammes vibratiles de chaque côté alors qu'il en existe quatre chez la femelle comme l'a figuré WEBER; mais mon observation sur le vivant n'a pas été assez prolongée pour



que je puisse affirmer l'absence de la quatrième. Le tube digestif existe, mais en cul-de-sac et sans mastax; on n'y peut distinguer que deux régions, la première flanquée juste derrière la couronne de deux masses granuleuses, d'apparence glandulaire, la seconde à parois uniformément minces, renflée et terminée par deux ligaments qui semblent aller se confondre avec les muscles longitudinaux. Ce tube digestif n'est probablement pas fonctionnel; du moins était-il entièrement vide chez mon individu. Les deux masses latérales représentent-elles les glandes gastriques? Il est beaucoup plus probable, étant donné leur forme et leur rapports, qu'elles correspondent à celles que j'ai décrites dans le mastax. Le testicule occupe la moitié postérieure du corps; il est globuleux, à parois minces, renferment de nombreux spermatozoïdes de grande taille qui s'y remuent avec vivacité. De part et d'autre de son canal déférent existent deux petites masses rondes qui sont les glandes annexes dites prostatiques. Je n'ai pas vue le pénis evaginé."

Finally DE BEAUCHAMP mentions that *Otoglena papillosa* Ehrbg. may perhaps be identical with the male of *Eosphora digitata*.

The animal is common in many of the ponds near Hillerød; I have met with the male several times and convinced myself that I was only able to add little to the description of DE BEAUCHAMP. I only remark that I have not been able to observe any contractile vesicle; I have counted five transversal muscle bands; the two small glands on the sides of the rudiment of the mastax are found. As well known *Eosphora digitata* is a slowly swimming or creeping animal, and the male does not move much faster than the female; the hyalinity of the male is much greater than that of the female, but seen with a low power it much resembles a young female.

### *Copeus labiatus* Gosse.

Male: Weber 1897 p. 92. Pl. IV fig. 6.

Tab. II, fig. 1.

The mainpoints in WEBER's excellent description are as follows:

Cuticula thin, homogeneous. The general form of the male is that of an elongated cylinder, rounded in its anterior part, thickest in the middle and attenuated behind, ending in a foot with two short toes between which, as in the female, is placed a little "éperon". Two normal foot glands. The form of the body differs very much from that of the female which is much broader behind, abruptly finishing with a tail and well marked foot, the tail in the male being almost absent. Head a little broader than the forepart of the body. No gelatinous cover which is so characteristic of the female. No alimentary canal, only oesophagus represented by a transparent mass. Wheel-organ strongly reduced, only a single wreath of cilia, two feebly developed ears; it is doubtful whether there exists a ventral lip; the muscle system consists of a series of longitudinal muscles, retractors of the wheel-organ and of the foot, of muscles for the penis and suspensor muscles of the testis. A three-lobed brain is found; the central part is pyriform and carries the eye. There is a dorsal antenna and two large lateral antennæ, either with a tuft of cilia or with a single one. Four pyriform cells behind the wheel-organ and without connection with the brain. The excretory organ consists of two lateral canals each carrying five vibratile tags; contractile vesicle doubtful. Testis pyriform,



*Eosphora digitata* ♂.  
Ehrbg. after de Beauchamp.

large; penis short with a muscle sheath and prostata glands. Above the testis a hyaline ovoid mass regarded as rudiment of the alimentary canal; further some globules regarded as remains of yolk. Length of female 600–700  $\mu$ , male “plus petit”. Time: May, July.

**Description.** The form of the male differs rather from that of the female; there is no neck, no inflated posterior part and hardly any tail. It has an ellipzoidic form, faintly tapering in the posterior part; it ends in two well developed toes, between which a little protuberance is observed in the female. I have never found any gelatinous sheath, so characteristic of the female. The wheel-organ consists of a vertically placed convex disc with a row of short cilia. The auricles are well developed, but very often withdrawn; they are unfolded in swimming, but commonly withdrawn in creeping. On the disc a broad band of long cilia. I have never seen any rudiment of a lip, which is extremely well developed in the female. The brain is broad, carrying a red eye. The dorsal antenna has not been observed; it is mentioned in WEBER's text, but not found in his figure. The two lateral organs, provided with long, sensitive hairs, are very conspicuous. The retrocerebral organ is a large broad pouch, containing rounded or pentagonal vacuoles; at the sides are two small lateral lobes. No openings for the organ have been observed. No sure rudiment of the alimentary canal, but between the retrocerebral organ and the testis lies a peculiar large, rather hyaline globule also mentioned by WEBER; that this, as supposed by WEBER, is a remnant of the alimentary canal, is possible. The excretory organ consists of two long curled canals, provided with four vibratile tags; there is no contractile vesicle; openings for the canals have not been observed. There are two prostata glands near the beginning of the ductus seminalis and two smaller ones more posteriorly. The testis is large, almost globular. As far as I have been able to see, the ductus seminalis which is twisted debouches into a very distended much broader part wholly covered on its interior part with cilia. This part opens on the posterior border of the last segment. If and how it is used as penis, I do not know. WEBER's drawing indicates the same distension but also that, in his opinion, it has nothing to do with the genital opening. In his drawing the penis opens above this distension which is quite independent of the genital organ. In his description the organ is not mentioned. There are two normal foot glands. There are eight transversal muscle bands, five pairs of longitudinal muscle bands for the wheel-organ and two for the foot. These bands overlap in the middle line of the body. Length of female 6—700  $\mu$ , that of male ca. 300  $\mu$ .

In a little peat bog divided into a great many smaller pits at Strødam about three kilom. from Hillerød I found, in May, in the algæ coverings of the surface in one of the pits, *C. labiatus*, in the other, *C. pachyurus*; especially *C. pachyurus* was very common; for years the two pits have had no connection with each other. Having isolated about a hundred specimens of both species, some days later a few males appeared. In samples taken in directly from nature, I never saw any males. The colonies were observed in May, but as heavy downpours began in June, the animals became rarer and rarer and finally totally disappeared.

**Copeus pachyurus** Gosse.

Male: Dixon Nuttall 1893.

Tab. II fig. 2.

DIXON-NUTTALL (1893 p. 333 Tab. 15) has given a good description and fine drawings of the male.

"In general outline they are very much like that of a young female, are restless little fellows, and, unlike the females, seldom withdraw their auricles, but keep swimming in a somewhat spiral mode. The brain, as in the females, is three-lobed and of the same shape (though I am of opinion the two smaller lobes are a little more pointed, and in some cases slightly more granular or opaque). Each sac is filled with numerous cells, which give the covering or skin the appearance of being beautifully and evenly marked with a fine hexagonal pattern. This I have noticed is the case in the female too. The occipital antenna stands at the base of the long lobe of the brain, and I also find this in both genders. The eye is seated on a small ganglion, which rests between the two sides or small lobes, and under the long, narrow neck of the centre lobe of the brain. The cavity of the body, which in the female contains the mastax, stomach etc. is filled with a large empty sac. The lumbar tentacles, with their retractile setæ are the same as in the female. Four vibratile tags run down each side. The large sperm sac and protrusile, ciliated penis are obvious. I noticed the spermatozoa in active movement inside the sperm sac. The size overall is  $\frac{1}{95}$ ."

**Description.** Body shaped like that of the female but much more hyaline. The great fat, ventricose, tail highly characteristic of the female is but slightly developed in the male. As in the female the body is short and thick, constricted in the anterior part. The wheel-organ consists of a rather vertically situated convex disc, surrounded by cilia and two large auricles which, in contradistinction to the female, are almost always extruded. On the disc stand some bunches of long bristles; there is no lip. The brain is large, bilobed, carrying a large red eye and gives nerves to the dorsal antenna and the two lateral antennæ, lying in the posterior part of the body. The tips of the tubules carry strong setæ (this according to Gosse is not the case with those of the female). Just as in the female the retro-cerebral organ is highly developed, consisting of a large median lobe, constricted in front, and anteriorly with two much smaller lateral lobes. The interior of the large sac is filled with a great quantity of vacuoles, often, owing to the pressure, almost penta- or hexagonal. As staining methods have not been used I cannot give a more thorough description of the organ; the ducts and the openings for the organ I have not been able to detect. The so-called "granulations calcaires or bacterioides" (DE BEAUCHAMP) may be present, but may also be almost wholly absent. Of the alimentary canal there is only a rudiment between testis and wheel-organ. Lateral canals strongly curved with five or six vibratile tags. There is no contractile vesicle; the openings of the canals at the tip of the penis have not been seen. The testis is extremely large, almost globular, often placed laterally. The penis itself opens on the posterior border of the last segment; it is protrusile and the canal is covered with cilia; a bundle of cilia at apex; there are two large prostata glands and two large pedal glands. There are seven transversal muscle-bands, at all events four longitudinal



muscles and four pedal muscles, overlapping each other in the middle part of the body; there is no gelatinous enveloping. In different development in the different species I have found a peculiar structure of globules, arranged in something like a very widemeshed net of which I have tried to give an idea in the figure. Length of male 300  $\mu$ . of female 350  $\mu$ .

With regard to the males of the genus *Copeus* at our present stage of knowledge it may be established, that they are relatively highly developed organisms but differing from the females in having no lip, no gelatinous cover, no real tail, no alimentary canal and no contractile vesicle.

General remarks with regard to the Notommatidæ. It will be understood that our knowledge of the males of the large family of Notommatidæ is but slight; only a few of the males belonging to the genera: *Proales*, *Diglena*, *Copeus* and *Notommata* are well known. From the descriptions of WEBER, ROTHERT, ROUSSELET and now from my own it seems that the males in outer form rather resemble the females. The size is comparatively large, but always smaller than that of the female; in some of them f. i. *Proales Wernecki* both sexes are at birth almost equally large, whereas the female grows larger later on. The cuticula is always thin. A sort of lorica is present in *Diglena forcipata* (WEBER). In the peculiar male of *Hertwigia volvocicola* the foot is wholly absent; in the other males described, it is almost as well developed as in the female; the body is always extremely flexible, constantly changing its form. Where the wheel-organ has been more thoroughly observed, a ventrally curved cilia-covered disc of oblong often triangular form has almost always been found; it is bordered by somewhat longer cilia; auricles may be present, but most probably they are generally slightly developed.

It is very interesting that the alimentary canal either seems to be developed in almost the same degree as in the female or, at all events, with conspicuous rudiments; in *Proales Wernecki* even the mastax and the small gastric glands are present. In the other species a longitudinally folded band or sac, lying above the testis, is often and most probably always observed; in some of them gastric glands may be present, a more thorough examination will most probably always show the lateral antennæ. It will be of great interest to know the developmental stage of the retrocerebral organ which according to DE BEAUCHAMP's investigation, just in the females of Notommatidæ, has reached so high and so peculiar a development. Our knowledge with regard to the organ in the males is at present extremely small; only of the male of *Copeus pachyurus* there exists a figure seen laterally (DIXON NUTTALL 1893 Tab, XV) in which the whole organ is well drawn. Most probably this figure has been unknown to DE BEAUCHAMP. The figure shows a long club-shaped sac strongly attenuated in the forepart and with two lateral sacs. Behind, the sacs are filled with a granular mass, more anteriorly with something like a reticulated tissue. The two openings for the organ I have seen in a conspicuous position in *Notommata aurita*. The excretory organ presents no peculiarities; the two lateral canals carry from

three to six vibratile tags; a contractile vesicle is hardly ever observed with certainty (*Cyrtonia*: ROUSSELET). The testis is formed as in most of the rotifers; prostata glands are almost always present; the ductus seminalis opens upon one of the first foot joints; commonly it is the same organ which when turned inside out is used as penis. Only in the *Diglena*-species do we find a highly complicated structure, a real penis differing much from what we commonly find among the Rotifers. The muscle system seems in the whole family to be of a very conform structure; it is always highly developed, especially the transversal muscle bands are very conspicuous and are present in a number from five to seven. Conglomerates of opaque corns are almost always observed over the testis. Two foot glands seem always to be present. As far as I have seen, most of the males of *Notommatidae* are almost just as slowly creeping or slowly swimming animals as the females; only the males of *Diglena* are vigorous swimmers. They are difficult to detect, many of them resembling young females. For that very reason I suppose they are so rarely observed.

### Hydatinidæ.

The family *Hydatinidae*, as I understand it, comprises only three genera *Hydatina* with *H. senta*, *Rhinops* with *R. vitrea* and *Notops* with *N. brachionus*. Of all the three species the males are known; that of *N. brachionus* however only slightly. Best described of all Rotifera males is that of *H. senta*.

#### *Hydatina senta* Ehrbg.

Male: Ehrenberg: 1838 p. 412.

Leydig: 1855 p. 98.

Cohn: 1856 p. 435.

— 1858 p. 284.

Leydig: 1857 p. 410.

Plate: 1886 a p. 36.

Weber: 1888 p. 42.

Female: de Beauchamp: 1909.

Martini: 1912 p. 425.

Tab. VIII, fig. 1—2; Tab. IX, fig. 1—6; Tab. X, fig. 3—4.

As well known the female, anatomically as well as biologically is one of the best studied Rotifera of all, especially owing to the admirable investigations of DE BEAUCHAMP (1909) and MARTINI (1912 p. 425).

As mentioned above the male was already described by EHRENBERG but as a special form: *Enteroplea hydatina*; LEYDIG, COHN, PLATE and WEBER have all contributed to the study of its anatomy. It was my intention to use *Hydatina* as the main form on which to base all my studies of the males of Rotifera. The male was found in 1901 in a single pond; this was filled up and I did not see the male again before 1920. According to my experience *H. senta* is restricted to very slowly outdrying pools, polluted by outflows from dung-hills; further it is only to be found in the early spring. Of these two points I had no clear understanding before the spring of 1920.

Combining the descriptions of the above-named authors the male may be described as follows.

The body has exactly the form of that of the female, the skin is softer and more hyaline. Earlier authors have only rather cursorily studied the wheel-organ, but WEBER has shown, that it possesses five lobes, situated dorsally and equipped with rather long cilia, but they are not so well developed as in the female. Whereas the wheel-organ in the female is almost triangular with a deep notch ventrally and medially, the triangle in the male is much lower (WEBER, PLATE), the borders equipped with a series of long cilia. The mouth is closed, of the alimentary canal only a band remains, the function of which is only to support the testis. In it yellow or brown bodies, most probably fat oil, are found (PLATE). The muscle system is highly developed; the transversal muscles are numerous (WEBER); of the longitudinal muscles, the strong retractors of the wheel-organ, the muscles of the foot, and the transversally striped muscles of the penis, are especially mentioned. The nervous system consists of a large brain giving off two nerves for the dorsal antenna; lateral antennæ are only observed by PLATE. On the brain a circular light-refracting but not red spot is regarded as the eye. Of the excretory system the two long canals equipped with four vibratile tags are observed; the canals possess two openings one upon each side of the penis; the openings are round and surrounded with short and stiff cilia (PLATE and WEBER). There is no commissure between the canals and in accordance with PLATE and WEBER but in contrast to earlier observers no contractile vesicle; the foot glands are in accordance with those of the female. The testis is piriform enveloped in a thick muscular layer (COHN, WEBER not LEYDIG). It is fixed to the body wall by means of three pairs of ligaments; the base of it is longitudinally striated; at this base the penis is attached; it consists of a sheath transversally striated by fine and numerous muscles; it is cylindrical and long. The external orifice is surrounded by a crown of short cilia; in this thick sheath lies the real penis, a very thin pointed organ (WEBER). At both sides of the penis two glands commonly regarded as prostata glands are observed. On both sides of the testis and above it opaque granular masses, according to COHN, WEISSE and WEBER remains of the yolk, according to LEYDIG urin concretions, are observed. Size of female 4–500  $\mu$  of male 200–250  $\mu$ . Time March–May.

**Description:** Body form almost that of the female, but the dorsal side somewhat more vaulted. Cuticula extremely thin and the whole animal extremely hyaline. Foot short, confluent with the body; two short acute toes. Wheel-organ highly differentiated, still not so much as that of the female. The ciliary wreath (couronne postorale of the authors) constitutes a band of short, very fine cilia, in which I have not hitherto been able to point out the strong sensorial hairs mentioned by DE BEAUCHAMP in the wreath of the female. It encircles a disc somewhat ventrally placed. This disc, which is triangular in the female, is of a somewhat different form in the male, the ciliary wreath on the ventral side only forming a great curve. In the female the mouth is situated in a furrow, lying a little above that point where the two sloping sides of the ventral contour of the disc meet each other; the furrow and part of the disc above this is covered with fine cilia. Where the mouth opening is situated in the female, there is a cupshaped cilia-covered elevation, carrying on its top about 10 strong setæ. The other part of the disc seems to be destitute of any cilia coating, but carries strong setæ (membranelles DE BEAUCHAMP) in an arrangement similar to that in the female, though somewhat reduced. On the disc nearest to the dorsal side stands a series of five elevations, of which the median is



the most conspicuous, carrying on its top 7—9 membranelles; laterally to it are two others, carrying about six membranelles of different size. All this is in close accordance with what we find in the female; more ventrally in the same place, as in the female, but more reduced are found two convergent lamelles, bearing on their borders series of membranelles, diminishing in size dorsally ventrally; above these membranelles again are two other elevations with a series of hairs, much more developed in the female than in the male. The two series of strong hairs which border the mouth opening dorsally, I have not been able to find in the male. The hypodermal cells of the corona have not been studied.

The brain is rectangular, giving off nerves for the wheel-organ, but neither they nor the retrocerebral organ have been subjected to a close inspection; the last named seems to be very small, resembling in form that of the female; the openings have not been detected. From the brain proceed nerves for the dorsal organ and from the hind corners the long nerves for the lateral organs. I have hitherto been unable to detect the two muscles which go to the dorsal organ in the female, though they are most probably present. As in the female we find no eye spot. As all other authors have pointed out, there is no alimentary canal. In accordance with LEYDIG (1857, p. 411) the suspensor testis (COHN) may however be regarded as a rudiment of the alimentary canal. Seen laterally it may be shown that the suspensor testis, which extends forward from the frontal border of the testis to the hypodermal cells of the wheel-organ, being fastened just where the mouth parts are to be found in the female, is directly continued in the remarkably well developed indusium, which is fastened dorsally to the transversal muscle bands at three to five points, and in which further the testis is suspended. The form of this indusium differs from specimen to specimen; it can only be observed laterally and has been well figured by WEBER (1888, Pl. 33, fig. 2) and mentioned by LEYDIG (1857, Tab. 16, fig. 3—4).

When WEBER states that the indusium is to be regarded as a real "réseau musculaire", and that it is enveloped "par la continuation des masses granuleuses représentant des rudiments du tractus intestinal" this is rather difficult to understand from a histological point of view. LEYDIG's supposition, that the suspensor testis and the indusium are parts of the rudiment of the alimentary canal, is more intelligible, inasmuch as, according to him, it is said to contain "grosse Blasen mit Häufchen solcher gelbbraunen Körner welche die Magencellen aller Rotatorien erfüllen". The real connection between the testis, its modus of suspension and the real derivation of the suspending tissues can only be studied in cuts.

The excretory organ consists in two lateral canals which, directly below the hypodermal cells of the wheel-organ, anastomose with each other, and are provided with two slings, the one immediately below the wheel-organ, the other a little more in the middle of the body; there is no contractile vesicle though curiously enough it has been indicated by all the earlier authors (COHN, LEYDIG, DADAY and HUDSON). WEBER supposes that they have seen with "les yeux de la foi" (1888 p. 43). It is much more probable that, with the more primitive instruments at their command, they have

regarded some parts of the indusium or of the sac, filled with opaque corns, (often almost empty) as the contractile vesicle; PLATE and WEBER state correctly that there is no contractile vesicle; the two canals debouch directly on both sides of the genital opening. Special setæ round the two openings (PLATE, WEBER) I have not been able to see. As in the female so also in the male on both sides we really find two canals; the straighter one carries the vibratile tags to a number of four, the other is secretory and exhibits numerous slings; how these two canals are connected with each other, I have not been able to elucidate.

The testis is large, pyriform, containing numerous spermatozoa of two different kinds, the acute staff-formed ones are here always lying in the place, where the testis passes into the ductus seminalis; this is long, in its interior covered with cilia and provided with two prostata glands of very different size. The ductus seminalis is further transversely striped with fine and numerous muscle bands. This has also been seen by WEBER who further states, that it is only a thick cuticular sheath, containing in its interior the true penis, "cordon fin, delicat et très pointu" (1888 p. 45). I have always been quite unable to see anything of that. The ductus seminalis opens dorsally at some distance from the toes; more than once I have seen the evaginated ductus seminalis surrounded by a crown of cilia turned out; I am inclined to think that, in *Hydatina senta* just as in most of the *Notommatidae* there is no real penis, but that it is the ductus seminalis which, turned inside out, is used as such (Tab. X, fig. 3). There are two very large foot glands.

The muscle system is highly developed; in the figs. 1—2, Tab. VIII I have tried to give a sketch of it; compared with the figures of MARTINI (female) it will be seen, that there is great accordance between his and my drawings; but on the other hand also some very conspicuous differences. As the muscle system has been studied only upon living animals I do not think it is correct to go into details, in as much as I hope that a more elaborate study of the anatomy of the male will appear later on. I only wish to remark that, also in the male, the muscles of the forepart and those of the hindpart overlap each other in the middle line of the body. When the animal has been lying under pressure for some hours and is almost dying, a moment arrives, when some parts of the muscles are extremely conspicuous. This is especially the case with the transversal muscles. In Fig. 1, Tab. IX I have tried by means of the camera to give as thorough a drawing of the transversal muscles as possible. The figure shows the peculiar manner in which these transversal muscle bands are connected with each other and are provided with large nuclei, situated in expansions of the bands. When comparing the figure with those of ZELINCKA of *Discopus* I have now and then thought that I had to do with some parts of the sympathetic nerve system, which has only been observed by him, but continuous examinations have convinced me that this was not the case.

Above the testis there are from one to three hyaline sacs containing a number of opaque corns of different size and numbers; these sacs are in accordance with those which are almost always found in the males and very often in the females,

especially in the young animals. As well known, especially with regard to *Hydralina*, LEYDIG has regarded the corns as urine concretions, and the sac itself as a rudiment of the alimentary canal. WEISSE and COHN regard them as yolk masses, deriving from egg. WEBER follows the last named authors. Size of female 4—500  $\mu$ , of male 200—250  $\mu$ . Time: March—May.

### ***Rhinops vitrea* Hudson.**

Male: Rousselet 1897 a, p. 6.

Tab. X, fig. 1—2.

ROUSSELET (1897 a, p. 6. Pl. I) describes the male as follows:

The shape of the male differs somewhat from that of the female; the body becomes suddenly narrower in the lumbar region, whilst in the female it tapers very gradually down to the toes. The body is very lithe and soft, bending constantly in every direction. The corona with its proboscis-like dorsal projection resembles that of the female in every way, and two red eyes are in the same manner situated near the extremity of the proboscis, each having a minute spherical crystalline lens imbedded in the red pigment. A dorsal antenna is seen on the dorsal side, a little below the eyes, and the two lateral antennæ are very conspicuous at the projecting angle of the lumbar region each furnished with a brush of abnormally long setæ; in the female the lateral antennæ are very small. The foot is short, consisting apparently of one joint containing the two foot-glands, and terminating in two minute toes. The chief characteristic and the most abnormal feature about this male is the possession of functional jaws and intestine. The jaws are like those of the female in structure, but in one specimen I thought the right malleus shorter than its companion on the left side. The oesophagus is a thin, narrow tube leading to an elongated thick-walled stomach, with two gastric glands attached, and continued behind into a narrow intestine, all ciliated in the interior. The jaws were frequently moving, but the contents of stomach and intestine were very slight and of a greenish tinge, without solid particles of large size. It seems clear, however, that the male of *Rhinops* can take in some food, and therefore sustain life and live longer than all other known male Rotifers. There is a rounded spermsac, at the lower end of which the spermatozoa could be plainly seen in motion, terminating in a duct with the usual retractile and ciliated copulatory organ. A small contractile vesicle and lateral canals with flame cells attached are present as usual. Size of male 188—212  $\mu$ . Size of female 300  $\mu$ . Time May.

**Description:** Body more elongated than in the female; it becomes suddenly narrower in the lumbar region, whilst in the female it tapers very gradually down to the toes; the foot very long. The body is very soft and extremely hyaline. As in the female a long clubshaped proboscis proceeds dorsally; it can be more or less distended and retracted. When living it is always distended, but when the animal is dead, it may almost wholly disappear, and especially when the animal is seen laterally, be very inconspicuous. In these animals also the foot is withdrawn, so that it seems much smaller than it really is. (See Tab. X, fig. 2.) Wheel-organ highly developed and very difficult to study. It consists of a ciliary wreath, provided with two flattened, large auricles; dorsally it is almost interrupted, not coating the sides of the proboscis; ventrally it shows a deep furrow. On the disc another ciliary wreath, running from the sides of the proboscis in great curves downwards and meeting the above-named furrow. Where these two ciliary wreaths meet each other.



lies the mouth; between the two wreaths laterally two lobes carrying bunches of cilia. The proboscis itself at the corners with two bunches of strong cilia; itself on its whole under surface covered with a coating of very short fine hairs. A fully developed alimentary canal with well developed mastax, furnished with trophi of quite the same structure as in the female; a rather short oesophagus, a large stomach with thick walls; to them are attached two coneshaped, gastric glands. There is further a conspicuous intestine, but I have not been able to see any anus. Like ROUSSELET I have seen the jaws move. There is a large brain, sending off nerves to the proboscis and dorsally to the dorsal antenna; two lateral antennæ are present. In the proboscis there are, as in the female, two red eyes, furnished with lenses. There are two lateral canals, carrying four, perhaps five, pairs of vibratile tags. I have not been able to see any contractile vesicle, as observed by ROUSSELET. There is a large testis with two pairs of prostata glands; ductus seminalis long, coated with cilia and opening in the hind part of the first foot joint, carrying a double row of cilia, second foot joint with two long foot glands; two very short toes. There are nine transversal muscles, and a very complex system of longitudinal muscles for the wheel-organ, the foot, the penis and the testis. The course of these muscles will best be studied in the figure. Size of male 300—360  $\mu$ , of female 360—400  $\mu$ .

*R. vitrea* is found in about ten small ponds, all rich in organic matter and very often of a green colour; a few times I have also met with it in the pelagic regions of peat bogs. It is a spring form which appears in the middle of April often disappearing already in May, lying all the rest of the year as resting eggs.

### **Notops brachionus Ehrbg.**

Male: Hudson-Gosse: 1889 II, p. 12.

Montet: 1815, p. 320.

Tab. X, fig. 5—6.

HUDSON-GOSSE (1889<sub>II</sub>, p. 12, Pl. XV, fig. 1 b) figure and describe the male.

It is very unlike its mother in shape and size; a side view shows that the head slopes back to a hump on the apex of which is a bunch of tactile setæ. A nerve-thread from the nervous ganglion passes to these and lies between two fine muscular fibres. A moderately sized sperm-sack ends in a ciliated penis, just above the foot, which contains two large club-shaped glands. Close to the sac is a small contractile vesicle, the lateral canals of which can be traced on either side of the ventral surface.

MONTET (1815, p. 320, Pl. 12, fig. 31) gives a figure of the male but no description at all. He has seen the testis, the foot glands and excretory organ, the wheel-organ is represented as a circle of cilia with three hair-pads on the disc and two strong tactile hairs. As far as I can see two small tubercle-like protuberances without cilia are present. There is a rudiment of the alimentary canal containing a round body (most probably an oilglobule).

Description: Body almost broadest anteriorly, tapering behind with a peculiar

hump dorsally, a well developed three joint foot; cuticula very hyaline. Wheel-organ a ciliary wreath encircling a disc in the middle with a broad elevation, carrying along its borders a series of long hairs. Of the alimentary canal a large ligament which embraces the testis and reaches the corona; it seems to contain a number of small oilglobules. There is a large brain with a red eye and two nerves which run up to the dorsal antenna, situated upon the top of the hump. Two lateral antennæ. The excretory organ consists in two curled lateral canals with three or four vibratile tags, but I have not been able to find any contractile vesicle. Testis very large, containing two sorts of spermatozoa; it is suspended by means of a ligamentum or inducium; on the dorsal side, the ligamentum is fastened at four or five points on the transversal bands. Two prostata glands. Genital opening dorsally on the first foot joints; ductus seminalis coated with cilia and a bunch of cilia round the opening. A large oilglobule over the testis. At all events three pairs of longitudinal muscles for the wheel-organ and six or seven very conspicuous transversal muscle bands. In the foot two foot glands. Size: male 160  $\mu$ , female 450  $\mu$ .

*Notops brachionus* which seems to be a rare animal everywhere, is never found in this country. I have vainly been in search of it for many years. The males which have been used for the above given description have kindly been forwarded to me by Dr. ROUSSELET in 1907. He sent me some females which arrived safe and laid male eggs; a few males were hatched. Later on Mr. F. E. Cocks has been kind enough to forward to me two slides of males and a drawing. By means of this foreign material the above given drawings have been worked up.

#### General remarks.

It is characteristic of the males of this interesting family that they are only slightly reduced; the size is only about half that of the female; more in *Rhinops*, not quite so much in *N. brachionus*. The form is the same as that of the female; this especially holds good for *Rhinops* and *Hydatina*. The wheel-organ resembles that of the female sex and in *Rhinops* is almost identic in the two sexes. *Rhinops* is one of the few known Rotifers with full development of the alimentary canal, with mouth, mastax, gastral glands and intestine (anus?). In the two other species only the common rudiment exists; a brain with dorsal and lateral organs is most probably always present; the eye is wanting in *Hydatina senta*; traces of retro-cerebral organ most probably present; further investigations necessary. Two lateral canals with three or four pairs of vibratile tags; no contractile vesicle; a large testis, prostata glands, no real penis; the ductus seminalis turned inside out, when used as such. Sacs with opaque contents often or always over the testis. Highly developed muscle system, which needs further investigation.

#### Brachionidæ.

The family contains the three genera: *Noteus*, *Brachionus* and *Schizocerca*; only the males of the genus *Brachionus* are hitherto known.

### Brachionus.

Of the ten males of Rotifers which GOSSE (1856, p. 313) described and figured in his famous work, the seven belonged to the genus *Brachionus*. Some of these seven species (*B. amphiceros*, *dorcas*) are unquestionably only temporary forms of the same species. It is not possible, from the description and drawings, to distinguish these species in the male sex from each other. It is stated with regard to these males that the lorica is only feebly developed, that the head is more or less conical, set with large setiform cilia all over the front, that behind the front there are several lobes, with a red eye commonly on the truncate apex of the posterior lobe. The body cavity is filled behind with a mass in the middle of which is situated the group of opaque white granules, contained in an irregular bladder. The central part is occupied by the spermatheca, connected by a bottle-like neck with the head-mass, where a distinct corrugation probably marks an orifice, closed by a sphincter, which leads to the discharging duct. The spermatozoa are observed (about thirty). With the spermatozoa are extruded many spicula-like bodies. The penis is thick and united to the foot, terminating in a short truncate tube, the excretory organs are seen and described as a chain of irregular masses, running down from the head to the posterior part of the body, extending down into the penis-foot.

Even if it is impossible to distinguish the different *Brachionus* males, which GOSSE has described and figured, he who has observed the males of *B. angularis* and *B. dorcas* (= *B. pala*) will unquestionably understand, that GOSSE really has observed and figured the males of these two species. Quite correctly GOSSE described the male of *B. angularis* as covered with a tortoise-like lorica, and states that there is a conspicuous constriction between head and body, and that all internal organs are invisible, the interior being occupied by a vast number of minute granules or globules, irregularly clustered. In contrast to this little opaque male (length  $\frac{1}{40}$ th) stands the large, highly hyaline male of *B. dorcas*, measuring  $\frac{1}{20}$ th of an inch in length and very well figured (fig. 18—19) and described.

Hitherto the following *Brachionus* males have been observed:

- |                        |                                |  |
|------------------------|--------------------------------|--|
| <i>Brachionus pala</i> | Ehrbg. . . . .                 | GOSSE (1856, p. 316, Tab. I, fig. 2); WEBER (1898, p. 672, Pl. 23, fig. 16); PLATE (1886, p. 67, Pl. 3, fig. 25).                        |
| —                      | <i>urceolaris</i> O. F. M. . . | COHN (1856, p. 470, Tab. 24, fig. 8—9); WEBER (1888, p. 56, Pl. 35, fig. 2; 1898, p. 678, Pl. 23, fig. 20); TOTI (1861, Tab. I, fig. 9). |
| —                      | <i>Mülleri</i> Ehrbg. . . . .  | GOSSE (1856, p. 319, Tab. II, fig. 20).  |
| —                      | <i>angularis</i> Gosse . . . . | GOSSE (1856, p. 317, Tab. I, fig. 13—14).  |
| —                      | <i>Bakeri</i> O. F. M. . . . . | GOSSE (1856, p. 318, Tab. I, fig. 12). ROUSSELET 1897, p. 328, Pl. 16.   |
| —                      | <i>rubens</i> Ehrbg. . . . .   | ROUSSELET (1907, p. 153, Pl. 12, fig. 11).   |
| —                      | <i>quadratus</i> Rousselet . . | ROUSSELET (1907, p. 150, Pl. 12, fig. 7).  |
| —                      | <i>sericus</i> Rousselet . . . | ROUSSELET (1907, p. 149, Pl. 11, fig. 4).  |
| —                      | <i>furcatus</i> . . . . .      | THORPE (1891, p. 301); ROUSSELET (1906, p. 397, Pl. XIV, fig. 5).  |



**Brachionus pala** Ehrbg.

Male: Plate 1886, p. 65.

Weber 1898, p. 672.

Pl. XI, fig. 1—3.

PLATE (1886, p. 67, Pl. III, fig. 25) describes the male under *B. amphicerus*.

The wheel-organ is described as follows: "Der Räderorgan besteht aus einem continuirlichen Wimpersaume, über den der Kopf halbkugelig vorspringt. Auf der ventralen Hälfte dieser Calotte befinden sich noch eine Anzahl Cilien, deren Stellung und Grösse die Zeichnung veranschaulicht. Die stärksten unter ihnen sind an der Spitze oft zerfasert." There is a rudiment of an alimentary canal: "Zwischen der Unterseite des Gehirns und der Rückenseite des Hodens spannt sich als ein unregelmässiges Band der rudimentäre Darm aus. Das dies Gebilde eine solche Deutung verdient, geht daraus hervor dass sein hinterster Abschnitt, der also dem Enddarm entsprechen würde, blasenartig erweitert ist und dieselbe schwarze Körnermasse enthält, wie sie im Darm der jungen Weibchen vorkommt. Bei manchen Exemplaren ist der Zusammenhang zwischen der vorderen und hinteren Hälfte des rudimentären Darmes freilich nicht mehr vorhanden oder sehr undeutlich geworden." Brain with red eye; one dorsal and two lateral antennæ. Two lateral canals, no contractile vesicle. Testis normal, penis longer than foot; two foot glands.

WEBER (1898, p. 672, Pl. 23, fig. 16) gives a short description of the male. His figure shows that he has seen the lateral canals, and four transversal muscle bands; his drawing of the wheel-organ resembles mine; laterally round the forepart of the testis are drawn two organs which I have not been able to find and the function of which I do not know.

Description: Body cylindrical, provided with a short, inconspicuously divided foot, with two small toes. A faintly developed lorica, consisting of a larger dorsal and smaller ventral plate. No spines. The lorica very hyaline. The wheel-organ and partly the foot can be withdrawn in it. A terminally placed wheel-organ, consisting of a ciliary wreath, encircling a disc with three cushion-shaped elevations, carrying a number of long, rather stiff cilia; further six strong setæ. Of the alimentary canal only a rudiment, used as ligamentum for the testis. A large brain with a red eye spot; two dorsal nerves, running to one single dorsal antenna and two lateral antennæ far behind. Two conspicuous lateral canals with three pairs of vibratile tags; no contractile vesicle. Testis large, pyriform, with two kinds of spermatozoa; ductus seminalis in its anterior part coated with cilia. Penis, when not used, withdrawn; opening dorsally on the foot; when fully extended, thick, enormous, wrinkled, tapering behind, ending in a body like a glans, provided anteriorly with a wreath of long cilia. Ductus seminalis in its posterior part consisting of a chitinous tube, a real penis, disc-shaped at apex and here bearing an opening. When fully extended, the whole organ is much longer than the small foot, which hangs down ventrally as a lateral appendix of the penis. When not used, the whole organ disappears in the foot; it is pressed out, not so much by means of muscles as by means of blood pressure. When it is fully extended the wheel-organ is withdrawn. Two prostata glands. In the middle part of the penis two other glandlike bodies. Above the testis a globular light-refracting body, containing numerous sharply edged opaque grains, any connection with the rudiment of the alimentary canal I have never

been able to see. Strong, well-developed retractor muscles for the wheel-organ; from six to seven transversal muscle bands. Size male 120  $\mu$ , female 250—400  $\mu$ .

**Brachionus urceolaris** O. F. M.

Male: Cohn 1856, p. 470.

Weber 1888, p. 56.

Tab. XI, fig. 4.

COHN (1856, p. 470, Tab. 24, fig. 8—9) has given a good description and two fine small figures of the male.

He correctly states that there are no lorica and spines; a short foot; a wheel-organ consisting of a ciliary wreath, encircling a disc with long stiff setæ. No opening for the mouth; no trace of alimentary canal. A testis with stiff walls, which most probably are of muscular structure. A penis almost of the length of the foot. The canal and the opening of it carries cilia. The foot is annulated and carries two small toes. Foot glands present. Lateral canals with vibratile tags and a contractile vesicle. A brain with a red eye. Above the testis a mass of opaque grains, regarded either as part of the sexual organs, or as a remnant of the yolk.

WEBER (1888, p. 56, Pl. 35, fig. 2 and 1898, p. 678, Pl. 23, fig. 20) has figured the male; he has only had one single specimen. He especially pays attention to the following fact:

“Si les mâles n'ont pas de cuirasse complètement formée comme la femelle, ils ont cependant une enveloppe chitineuse analogue” une cuirasse modifiée, qui n'avait pas encore été mentionnée. C'est une cuticule beaucoup plus dure que celle des autres mâles, observés jusqu'ici. WEBER has not had occasion to see the vibratile tags of the excretory canals. There is no contractile vesicle, but prostata glands.

With regard to the wheel-organ WEBER says: “Je n'ai pu distinguer les couronnes ciliaires de la femelle; cinq lobes seulement se montraient à différentes hauteurs. De chaque côté, on voit deux petits cônes, surmontés d'un long cil tactile et plusieurs touffes ciliaires.”

*B. urceolaris* Ehrbg. var. *rubens* Ehrbg. Description. Body as in *B. pala*, not so hyaline; lorica consisting of a dorsal and a ventral plate; the first-named the largest. The wheel-organ can be withdrawn into the lorica. No spines. Foot short, consisting of only one joint; two toes which are very acute and better developed than in *B. pala*. Seen ventrally, the wheel-organ as in the female shows a conspicuous cleft; on the disc are four cushion-shaped elevations dorsally, with strong stiff cilia, and more ventrally a single cushion with a bunch of bristles; on the disc further two, perhaps four strong setæ. The brain is very large. With regard to rudiment of alimentary canal, antennæ, lateral canals, testis, penis and foot glands I find no differences between *B. rubens* and *B. pala*. The longitudinal muscles have a somewhat different course. The penis may be protruded just as in *B. pala*; it is then of quite the same form and composition; on the figure it is shown withdrawn. Size male 120—130  $\mu$ , female 250—280  $\mu$ .

*B. rubens*, which is often regarded as a variety of *B. urceolaris*, (not by ROUSSELET 1907, p. 151) has the peculiar custom almost always to fasten itself to the carapace of the parthenogenetic generations of *D. pulex*, coating them with a thick mantle. It is a pronounced pond form; I have only met with it in late spring and midsummer.

**Brachionus quadratus** Rouss.

Male: Marks & Wesché 1903, p. 508.

Marks & Wesché (1903, p. 508, Pl. 26, fig. 1) describe the male as follows.

Stoutly fusiform in shape, a lateral view shows the head and foot curved downwards when swimming free. Head inclined to be globular, a little variable in shape, the constriction of the neck also varies with position. Head capable of retraction within the body. Body cylindrical, stout, has marks of the edge of the carapace, as in *Diaschiza*. A fold of skin is sometimes seen in dorsal view. Foot stout, short and wrinkled, tapering from body and retractile. Toes minute, triangular; sometimes a thread is spun from their extremities. Cilia long. Brain large, three-lobed on the front. Sometimes oval glands seem to form part of it, in dorsal view. Eye, rather nebulous, not well defined, faintly red, and variable in shape. Antennæ dorsal, well forward on the head; lateral, low down on sides of body, as in the female, with long setæ. There is no digestive system. Lateral canals difficult to make out; at all events two flame-cells on each canal. Two well marked foot glands. A very large sperm sack tapering from the centre of the body cavity to the middle of the foot. A dark granular mass, contained in a vesicle shows above the testis in dorsal view. Size: male 127–141  $\mu$ . Time March 8th and 21st.

**Brachionus Bakeri** O. F. M.

Male: Rousselet 1897 c, p. 331.

ROUSSELET (1897, p. 331) says with regard to the males of the different varieties of *B. Bakeri*, that they cannot be distinguished from each other. This is unquestionably quite correct. I have often seen the males; but they differ only slightly from those of *B. urceolaris* var. *B. rubens*.

**B. angularis** Gosse.

Tab. XII, fig. 1–2.

Male: Description: Body elongate, provided with a very peculiar lorica, which Gosse very correctly mentions as tortoise-shaped. There is a rather small, narrow dorsal lorica and a much broader, but shorter ventral lorica, the posterior edge of which is not seen with certainty. An inconspicuous divided foot with two toes. No spines. Before the lorica a sharply defined part, carrying the ciliary wreath, surrounding a cone-shaped disc with about ten long, stiff cilia centrally and six long setæ. Owing to the thickness of the lorica it is very difficult to see the interior organs. No remains of an alimentary canal are observed. There is a brain with a red eye and a dorsal antenna and two lateral antennæ. Immediately below the shield, extending forwards from the dorsal antenna to the forepart of the lorica, is observed a peculiar elongate structure, consisting of small grains, present in all the males I have seen; it is possible that here we have a retrocerebral organ. Excretory organs have not been observed. With regard to testis, penis, ductus seminalis, prostata glands and sac with conglomerates, the structure of the male is in accordance with that of the other *Brachionis* males described. Only a few longitudinal muscles are observed and no transversal muscles. No foot glands observed. Size of male 90  $\mu$ , of female 200  $\mu$ .

*B. angularis* is, of all our *Brachionus* species, that which is most commonly



found in the pelagic region of smaller lakes; besides, it is a pronounced pondform occurring together with *B. pala*. With regard to sexual periods, maxima, number of eggs etc. it is in accordance with *B. pala*; still the cluster of male eggs is not so large, the number not being above from six to eight.

### *Schizocerca diversicornis* Daday.

Tab. XII, fig. 3—4.

Male: Description: Body somewhat flattened, almost rectangular. A well defined lorica, consisting of a dorsal and a ventral plate, the first provided with some peculiar elegantly curved lines (see figure). Lorica rather thick; no spines. A forepart which can be wholly withdrawn into the lorica; a relatively well-developed foot with two joints and two short toes. The wheel-organ consisting of a ciliary wreath, surrounding a cone-shaped disc; the top of the cone carries a strong bunch of long bristles; on the sides of the cone two strong, long setæ. Of the alimentary canal remains only a band running forward from the testis below the brain. This is extremely large, carrying a red eye; there is a conspicuous dorsal antenna and two lateral antennæ, lying near the posterior edges of the body. Owing to the thickness of the lorica I have not been able to see the lateral canals; there is no contractile vesicle. Testis very large; two large prostata glands. Penis of quite the same structure as described in *B. pala*, only when fully extended still larger and thicker. When not used, fully retracted.

A chitinous tube ending with a disc and glands round the tube; no special penis muscles. Dorsally, behind the dorsal antenna and over the posterior part of the testis two round globular masses, containing a number of opaque, sharply edged grains. Only some longitudinal retractors of the wheel-organ seen. Size of male 160  $\mu$ , of female 300  $\mu$ .

*Schizocerca diversicornis* is common in larger ponds and smaller lakes; it is here a pronounced plancton organism; it is a stenotherm summer form, with maximum at highest temperatures and sexual period in Aug.—September. The female carries one or two parth. female eggs, rarely more than four male eggs and one resting egg.

### General remarks.

In the structure of the males of the fam. *Brachionidae* I especially wish to call attention to the following facts.

The males are very small, strongly reduced. There exists, at all events in the two genera *Brachionus* and *Schizocerca*, a real lorica, consisting of a dorsal and a ventral plate; spines are always absent, and so also is all other equipment of the lorica (facetted structure etc.), even if these structures are highly developed in the female. The wheel-organ can be wholly retracted into the lorica, but commonly not the foot; this is always present, provided with two toes. The number and place of bunches of cilia and long stiff single setæ vary from species to species; a retrocerebral organ has never been observed with certainty. Rudiments of the alimentary

canal now used as ligamentum for the testis are most probably almost always present. The brain carries a red eye; dorsal and lateral antennæ are in all likelihood always present. In the excretory organ the contractile vesicle is absent; three or four vibratile tags; a large testis with prostata glands. Very peculiar is the structure of the penis; with regard to this point I refer to *B. pala*. Above the testis a conglomerate of opaque, sharp edged grains. It is of interest, that a series of transversal muscle bands can often be pointed out.

The males are all extremely quick and are hatched in great numbers in the sexual periods. Often I have had small clouds in the vessels, consisting almost entirely of newly hatched males.

### Anuræadæ.

The family *Anuræadæ* consists of the three genera *Anuræa*, *Anuræopsis* and *Notholca*. Apart from *A. aculeata* there exists no drawing or description of any male, belonging to this family; the male of the most common Rotifer, that of *A. cochlearis* has hitherto been unknown. ROUSSELET (1903, p. 176) states that the male of *N. heptodon* has been observed, but gives neither description nor figure.

### *Anuræa aculeata* Ehrbg.

Male: Plate 1886, p. 64.  
 Marks & Wesché 1903, p. 509.  
 Krätzschmar 1908, p. 630.  
 Montet 1915, p. 342.  
 Tab. XIII, fig. 1—2.

PLATE (1886, p. 65) with regard to the male says only as follows:

“Sie haben cylindrische Gestalt: vorn sitzt der Räderorgan, unter dessen Wimpern sich einige durch besondere Länge auszeichnen, hinten verjüngt sich der Körper zum Penis und endet mit flimmernder, breiter Spitze. Von den übrigen Organen habe ich leider nur den grossen Hoden und das Gehirn erkennen können, das ein dorsales Tastgrübchen versorgt und einen Augenfleck trägt. — Grösse 100  $\mu$ .”

*A. aculeata* var. *brevispina*. MARKS & WESCHÉ (1903, p. 509, Pl. 26, fig. 2).

The shape of this minute rotifer is inclined to be truncate, but globular, not so broad as it is long, and the body, unlike that of the female, in a foot, ends usually pendant. — Head stout, with a chitinous covering on the dorsal side, well marked in lateral view; this folds up and encloses the head when the animal retracts the cilia. There is a deep constriction at the neck. Body, enclosed in a carapace which has openings on the dorsum and sides, so that it appears to be enclosed in three more or less arched plates; in the specimens seen there was a conspicuous oil globule. The foot has a chitinous sheath, down which the passage from the sperm-sack passes, so that it may be said to take the place of the penis. At the extremity are two hyaline threads, as in *Triarthra*. Toes, none. Cilia fairly long. Brain, large occupying all the head and part of the body. Eye large, bright red, circular in dorsal view, narrow in lateral view, nearer the ventral than the dorsal side. Antennæ very minute on head and sides of carapace. No digestive system. No foot glands seen but the animal seems to spin a thread from foot. Vascular system very indistinct. No contractile vesicle. Generative system a large pouch containing spermatozoa and other bodies; the pouch narrows to a

long neck, which is worked up and down the foot, and is capable of protrusion from its extremity. Size male 84  $\mu$ . Time 2nd April.

KRÄTZSCHMAR (1908, p. 630, Tab. XIV, fig. 1—2) has given a very thorough description of the male and three interesting figures. His paper is of great interest, because his observations are based upon cuts; as far as I know, it is the first time a Rotifer male has been treated under microtome.

The main points in the description are as follows:

Body conical; a dorsal lorica with a median cleft; ventral side without lorica; wheel-organ can be withdrawn in the lorica by means of strong muscles. It presents no peculiarities. No alimentary canal; a large brain with a crimson eye; no antennæ observed; a large testis with spermatids and spermatozoa; penis large, in cross section oval; the ductus seminalis covered with cilia; two ventrally and two dorsally situated muscles. Over the testis a large oil globule. KRÄTZSCHMAR supposes that the function of this oil globule is to prevent the rotating motion in such a way that the swimming course becomes straight, the way being shortened in this manner, and the speed of the male sex being augmented. The phenomenon is due to the fact that the buoyancy of the oil globule is greater than the force which is used during the rotating motion. It is further of the greatest interest, that KRÄTZSCHMAR has been able to show by means of cuts, that this organ is in connection with the excretory organ. The oil globule is surrounded by a light-refracting sphere, which is further surrounded by an opaque mass of dark grains; the two lateral canals unite below the brain and dilate into a large sack, enveloping the oil globule and the surrounding cell masses; from the underside of the sack runs a canal which opens dorsally upon the animal in the median line; the opening is surrounded by a ring; the lumen of the canal is always conspicuous, and the walls are stiff; it is supposed, that there is always a connection between sack and outer medium. It is of special interest that KRÄTZSCHMAR has shown that the muscles are transversally striped. One pair of transversal muscles are observed. Size: Length of body 70  $\mu$ . Breadth 35  $\mu$ . Penis 20  $\mu$ .

MONTET (1915, p. 342, Pl. 13, fig. 39) figures the male, but gives no description at all; the figure is very difficult to understand.

Male: Description: Body broad, conical, tailless, broadest in the middle, and with a peculiar notch dorsally. A relatively thick cuticula, but no conspicuous lorica; this is most developed on the dorsal side. Ventrally is found a quadrangular plate from the edges of which lines run out to the sides of the body. In some individuals I think, I have seen a lorica, somewhat resembling that of *Salpina* with a median cleft running from a little below the wheel-organ downwards to the penis. But this line is not conspicuous in all individuals. The wheel-organ consists in a single ciliary wreath, slanting a little ventrally, encircling a disc with three bunches of longer cilia and four strong setæ. No alimentary canal; a very large, remarkably broad brain with a broad red eye spot. I have not been able to see any dorsal antenna. Two conspicuous lateral antennæ are situated in the posterior part of the body. Of the excretory organ I have only been able to see a short part, lying between brain and testis; it is provided with two vibratile tags; no contractile vesicle. Testis large, globular, with two sorts of spermatozoa. Penis well-developed, strong, rather thick, with two small muscles; ductus seminalis covered with cilia and round the opening a tuft of cilia; in the posterior corners of the penis two strong hairs. Well-



developed prostata glands. Above the penis remarkably large oil globules, and often a great many others, deposited round and especially above the testis. There are three pairs of strong longitudinal muscles for the wheel-organ and one shorter slanting pair, further smaller muscles for the penis. When compressed three transversal bands are observed. Size of male  $100\ \mu$ , that of penis  $20\ \mu$ . Size of female  $200\text{--}250\ \mu$ .

### ***Anuræa cochlearis* Gosse.**

Tab. XIII, fig. 3—4.

**Male: Description.** Body broad, conical, broadest in the middle, tailless. Cuticula thick with a rather well developed dorsal lorica, divided into three parts, a fore-part which consists of a transversally placed rectangular part and two lateral elytralike parts, separated from each other by means of a cleft. Ventral side without lorica. Wheel-organ consisting of a single ciliary wreath, slanting ventrally, surrounding a somewhat vaulted disc and provided dorsally with a bunch of long cilia. More ventrally, where the opening for the mouth is in the female, is a curve of long cilia. Four strong setæ. No alimentary canal. Brain large, with a red eye spot; a conspicuous dorsal antenna before eye and two lateral antennæ near the hind edges of the "elytra". Owing to the thick lorica the muscle system is difficult to observe. Two lateral canals with three vibratile tags, no contractile vesicle. Testis and penis constructed in quite the same manner as in *A. aculeata*. Special muscles for penis have not been observed. We find at the end of the penis two quite similar long setæ as in *A. aculeata*. Two small prostata glands. Above and around the testis a number of large oil globules; one of them, lying directly over the testis, is commonly much larger than the other. Size of male  $80\text{--}90\ \mu$ , of penis  $20\ \mu$ . Size of female  $160\text{--}200\ \mu$ .

### ***Anuræopsis hypelasma* Gosse.**

Tab. XIII, fig. 5—6.

**Male: Description.** Body elongate, very soft, hyaline without any distinct lorica but dorsally with two and ventrally with one deep longitudinal furrow. No foot. Wheel-organ almost vertical upon the longitudinal axis, consisting of a ciliary wreath, encircling a disc, which, when slightly compressed, especially seen ventrally, shows a central coneshaped and two lateral parts, the first equipped with about eight to ten setæ, the lateral ones with a bunch of long cilia; between the three parts two long strong setæ. No alimentary canal. Brain large with a large red eye. Neither dorsal nor ventral antennæ have been observed. Two pairs of longitudinal muscles, running from the wheel-organ to the root of the penis. Two conspicuous lateral canals with three vibratile tags each; no contractile vesicle. A rather small elongate testis surrounded by a large prostata mass. Penis of enormous and extraordinary length, more than half the length of the body, very soft, flexible; ductus seminalis very long, double-contured, with rather stiffened sides and ending in a cup-shaped body, surrounded by cilia; internally the canal is covered with long cilia. No setæ at apex. In

the penis itself two glandlike bodies the openings of which I have not been able to see. Between the brain and testis a very large constant oilglobule, and scattered in the body cavity many smaller oil globules.

Size: Male 80—90  $\mu$ , penis alone 30  $\mu$ . Size of female 120  $\mu$ . *A. hypelasma* is a typical pondform, only rarely met with in the pelagic region of larger lakes; it is a summerform, not appearing before May and with its maximum at the highest temperature. The female as well known carries one large oblique female egg; two or three small male eggs and a very large resting egg.

During the large maxima in August, Sept. the males have appeared in my vessels in great masses; even with slight magnifying powers they are easily recognisable owing to their large penis; swimming with enormous speed and always in straight lines, they seem to use the penis as a helm.

### *Notholca longispina* Kel.

I have seen the male in great numbers; it was on a journey, when I was only equipped with a very insufficient microscope; it resembled the males of *Anuraea* and had no spines.

### *N. acuminata* Ehrbg.

Tab. XIII, fig. 7.

Male: Description. Body elongate, very soft, hyaline without any distinct lorica neither dorsally nor ventrally; without any deep longitudinal furrows, behind with a large pouch of different form in the different specimens. No foot. Wheel-organ vertical upon the longitudinal axis, consisting of a ciliary wreath, encircling a disc carrying another interrupted row of cilia and a number of small hills, provided with bunches of bristles. No alimentary canal. Brain large, with a large red eye. Neither dorsal nor ventral antennae have been detected. There is no contractile vesicle, and the lateral canals I have observed are only very inconspicuous. Testis large with two sorts of spermatozoa. Penis extremely long, almost as long as the animal, faintly kneed, narrow, strongly tapering at apex, flexible. It is traversed by the seminal ducts, which are covered with cilia and near the testis provided with two small prostatic glands. As far as I have been able to see, there is not, as in *Brachionus*, stiffened sides and no cup-shaped body at apex. On the other hand I here found a peculiarly formed globular body hanging down from the apex. No transversal muscles and only three pairs of longitudinal muscles could be observed. The whole body was very opaque, containing large oil globules, especially in the posterior part.

For a long time I have been in search of the *Notholca*, males. Apart from *N. longispina* most of the other species seem to have their maxima at rather low temperatures, being most common in the winter half year. In April 1921, in one of the bays of the little river Susaa, near my summer laboratory, I observed that it contained enormous maxima of *N. acuminata*; they carried their eggs for a short time, but they very soon dropped off and were to be found at the bottom. The next

day, among some hundred isolated females in the margin of the vessels nearest to the window, I saw numerous males encircling the females and swimming with an extraordinary speed. Most probably the pairing took place during the encircling, lasting only a fraction of a second.

#### General remarks.

The males of the *Anuræadæ* are mainly characterized by having a rather feebly developed lorica, without facets and thorns of any kind; there is no foot, but an often very long flexible penis which cannot be withdrawn. The wheel-organ carries upon its disc some protuberances, carrying strong bunches of cilia or strong setæ often to a number of four. Any trace of an alimentary canal has never been observed. There is a large brain, most probably dorsal as well as lateral antennæ, but they are only rarely observed. A large red eye; no retrocerebral organ observed. Two lateral canals, but no contractile vesicle. Of great interest is the connection KRÄTSCHMAR has shown in *A. aculeata* between the excretory organ and the great oil globule above the testis; the excretory porus medially on dorsum is unique in the kingdom of Rotifera. The large testis opens in a thick penis; the ductus seminalis is covered with cilia; the opening with a bunch of cilia often with two strong setæ at apex. Prostata glands present. A well-developed muscle system, also transversal muscles. KRÄTSCHMAR has shown that they are striped in *A. aculeata*.

#### *Synchætadæ*.

The family comprises the three genera: *Synchæta*, *Polyarthra* and *Anarthra*. The genus *Polyarthra* was formerly referred to the fam. *Triarthradæ*. In 1899 (p. 135) I dissolved the family, referred *Triarthra* to *Pedalionidæ* and *Polyarthra* to *Synchætadæ*; DE BEAUCHAMP (1909 p. 28) has followed me in this. I still regard *Polyarthra* and *Synchæta* as nearly allied; on the other hand in many respects especially with regard to the wheel-organ, the differences are rather great, and after we have studied the structure of the males a little more closely, these differences have been augmented.

Only the males of *Synchæta* and *Polyarthra* are known. Both have been studied insufficiently by GOSSE and later on more thoroughly by PLATE (*Polyarthra*) and by ROUSSELET (*Synchæta*).

#### *Synchæta pectinata* Ehrbg.

Tab. III, fig. 1.

Male: Description. The body is conical, tapering behind, the skin very soft, hyaline, ending in a sharply defined foot, consisting of one rather large segment, carrying two short acute toes. The wheel-organ is only a ciliary wreath, encircling a terminally placed disc, covered with very short cilia; on this disc there are four strong hairs; no auricles are found; the two club-shaped prominences in front, so charac-



teristic of the female, are wanting. I have been unable to find any retro-cerebral organ, but there is a very conspicuous dorsal antenna, furnished with two nerves. The brain is large, carrying the large red eye. No lateral antennæ are seen; as ROUSSELET however has found them in some of the other species, they may possibly be present here too. There are seven or eight conspicuous transversal bands and powerful retractors of the wheel-organ. Above the testis is a large sac of different form, ending below the brain and reaching the penis behind. In the sac is always found a different number of rather large oil globules; in my opinion we here have a very conspicuous rudiment of the alimentary canal. There are two lateral canals which, in the specimens I have observed, seem to reach the brain. This is of interest, as the canals in the female sex do not reach much more than half-way into the body cavity. The canals carry four vibratile tags; there is no contractile vesicle, the canals opening on each side of the penis. The testis is very large of different form and size, provided laterally with two small prostata glands; the penis is remarkably small with a tuft of hairs at its base. There are two conspicuous foot glands. Size: Male 160  $\mu$ . Female 300  $\mu$ .

### ***Synchæta tremula* Gosse.**

Male: Gosse 1856, p. 321.

Hudson-Gosse 1889, p. 128.

Rousselet 1902, p. 283.

Tab. III, fig. 2.

GOSSE (1856 p. 321, Pl. XV, fig. 30—31) has given a short description which, together with the drawing, makes it very probable that he has really observed the male: An obconical form with rounded front, set with long cilia. A red eye, sharply defined, a central granular viscus, contained in a longitudinal cavity, in the bottom a large, irregular opaque white mass. The foot seemed to carry a great protrusile penis and to terminate in two minute toes. Size  $\frac{1}{2}$  in. HUDSON-GOSSE (1889 p. 128 Pl. XIII, fig. 2) have seen a glimpse of a male and also state, that they have seen the four styli on the coronal head.

ROUSSELET (1902 p. 283, Tab. III fig. 3 a). It is a small conical creature with a bent towards the ventral side, close behind the head. The front is truncate, with four styles. The red eye, dorsal antenna, large sperm sack and two acute toes are prominent. The mastax and stomach are quite absent, and replaced by the sperm sack. Size 110  $\mu$ . October.

Description. The male of *S. tremula* is most probably indistinguishable from *S. pectinata*. We find the same conspicuous rudiment of intestine (denied by ROUSSELET 1902, p. 283). It must only be pointed out that the foot is much smaller, only a small tap with inconspicuous toes but well-developed foot glands; it is perhaps placed more ventrally and the penis is somewhat more prominent. Size of male 120  $\mu$ , of female 250. — Time: May.

### ***Synchæta oblonga* Ehrbg.**

Male: Rousselet 1902, p. 287.

ROUSSELET (1902 p. 287, Tab. III, fig. 2 a). The description and figure of the male are not so plain that it can be distinguished from that of *S. tremula*.

***Synchæta littoralis* Rouss.**

Male: Rousselet 1902, p. 397.

ROUSSELET (1902, p. 397.) only says: "The male has been seen several times, and has much analogy with *S. oblonga*."

***Synchæta gyrina* Hood.**

Male: Hood 1887, p. 149.

HOOD (1887, p. 149) only says: "The male is a conical slender creature, 85  $\mu$ ."

***Synchæta tavina* Hood.**

Male: Rousselet 1902, p. 397.

ROUSSELET (1902, p. 397) gives no drawing. It is only stated that the brain is long with opaque granules at the tip of which red granules forming a double eye are imbedded.

***Synchæta neapolitana* Rouss.**

Male: Rousselet 1902, p. 410.

ROUSSELET (1902 p. 410, Tab. V, fig. 9b, c) has found the male. He only states: "It is of usual structure. Size of male 75, of female 109–163  $\mu$ ."

***Synchæta cecilia* Rouss.**

Male: Rousselet 1902, p. 407.

ROUSSELET (1902, p. 407, Tab. VII, fig. 16 b). The male of this species seems to be distinguishable owing to the large dorsal antenna, which is seen to emerge just above the red eye, and which is slanting backwards. Further the lateral antennæ are also conspicuous by their size, protruding low down at the sides of the body. Size of male 78  $\mu$ , of female 142  $\mu$ .

***Synchæta vorax* Rouss.**

Male: Rousselet 1902, p. 408.

Lie Petersen 1905, p. 20.

ROUSSELET (1902, p. 408, Pl. VIII, fig. 19 a) describes the male as follows: "The median tubular antenna, which is so prominent and characteristic in the female, is also present but of small size; in addition to this, the male has on the front two small tubular antennæ, one on each side, which is very strange. Further it has at the extreme front of the head but slightly ventral in position two stout fleshy, freely movable processes, surmounted by a broad brush of long stiff hairs. In no other males have I seen such organs." Size of male 149  $\mu$ , of female 272  $\mu$ .

LIE PETERSEN (1905, p. 20, Tab. I, fig. 5) gives a very good figure of the male, but no description. It seems that he has interpreted the alimentary canal correctly.

It will be seen that the males of the genus *Synchæta* are found rather frequently. Especially ROUSSELET has described and figured the males of several species, but as far as I can see all these males are not described in such a way, that they may be distinguished from each other; most probably the majority of them are really indistinguishable. Still it seems that there are two species *S. cecilia* and *S. vorax* which are characteristic.

Characteristic of all hitherto observed males is their conical shape, their often short foot, with two toes and well-developed foot glands. The wheel-organ is simplified to a terminally placed disc, surrounded by cilia, carrying on the disc the same four long hairs which characterise the females; auricles are absent and fleshy protuberances only observed in one species. A retrocerebral organ has not hitherto been observed; most probably dorsal as well as lateral antennæ are always present. Below the large brain a large red eye. Rudiment of alimentary canal hollow and often containing globules, most probably present in all species; it has hitherto mainly been overlooked, but it seems to have been observed by LIE PETERSEN in *S. vorax*; some of ROUSSELET's figures seem to show rudiments of the alimentary canal. Whereas PLATE (1886, p. 45) states that the length of the excretory canals in the females is very different, ROUSSELET (1902, p. 272) maintains that they always are very short in the male sex, not extending much over the anterior end of the gastric glands. In the males examined by me I have seen them reaching the brain. The testis is large, pearshaped; there are two short prostata glands; the penis opens dorsally: it is short and round, the opening provided with short hairs; the muscle system, especially the transversal muscles are highly developed.

### ***Polyarthra platyptera* Ehrbg.**

Male: Gosse 1856, p. 320.

Plate 1886, p. 18.

Tab. III, fig. 3—4.

GOSSE (1856, p. 321, Pl. XV, fig. 27—29). The small drawings give the figure very well and the comparison with a *Vorticella* is really excellent. Gosse says that the head is very large, with the body tapering quickly to the posterior part; both extremities are truncate. The front bears two warts, between which the rotatory cilia are placed, but the cilia (perhaps setæ) are longer on the warts. The hinder part is bifid, the smaller division being the caudal extremity or toeless foot, and the larger a protrusile truncate penis, ciliated at the tip. No internal organisation is discoverable. In one there was a globule in the middle of the great head. Towards the posterior dorsal parts a few irregular dark specks were visible, but generally the whole animal was clear, colourless, highly refracting, and showing an indistinct granulation. Its motions were swift and impatient, gliding about the field at headlong speed, occasionally remaining in one place for a few minutes, but not in stillness, for it was rapidly oscillating to and fro, and quivering.

PLATE (1886, p. 18, Tab. I, fig. 4) describes the male mainly as follows:

“In ihrer Gestalt weichen sie durchaus von den Weibchen ab und entbehren, wie fast alle Rädertiermännchen, einer Mundöffnung und eines Kauapparates. Die flossenartigen Anhänge des Weibchens fehlen völlig und auch von einem Augenfleck ist nichts am Gehirn zu erkennen . . . Die Männchen lassen eine Bauch- und eine Rückenseite unterscheiden, von denen diese etwas schmaler ist als jene. Beide hängen durch zwei nach innen gebogene Seitenflächen mit einander zusammen. Nach hinten verjüngt sich der Körper in den Penis, der am freien Ende bewimpert ist und während des Umherschwimmens teilweise eingezogen wird. Ein Fuss an den sich der Penis nach Gosse ansetzen soll, ist nicht vorhanden. Vorn bildet der Körper einen halbkugelig vorspringenden, einstülpbaren Kopf, der mit einem einfachen Cilienkranz und innerhalb desselben mit 2 Büscheln starker Wimpern besetzt ist. Der grösste Teil der



Leibeshöhle wird von dem Hoden eingenommen, der sich nach hinten in einen flimmernden Ausführgang fortsetzt. Neben dem Sperma, dessen feinere Structur bei der Kleinheit des Objectes nicht zu ermitteln war, liessen sich deutlich die unbeweglichen, schmalspindelförmigen Stäbchen erkennen... Der dem Hoden aufgelagerte rudimentäre Darm wies constant einige Fetttropfen auf. An dem ausleitenden Kanal des Spermasackes liegt eine Prostata ähnliche Drüse. Wassergefässsystem und Sinnesborsten vermochte ich nicht aufzufinden. Grösze 44  $\mu$ .

**Description.** Body almost globular, more or less acuminate behind, very variable in form, often when swimming with a globular forepart, sharply set off from a more acuminate cylindrical hindpart. No thorns, foot or toes. The wheel-organ seen from above, a cilia-covered cup with some stronger cilia laterally; from beneath a triangular space, dorsally carrying a series of long cilia, ventrally with a wreath of cilia, following the borders of the triangular space. In the middle of that a few faintly protruding hills carrying on their tops a bunch of cilia. I have been unable to confirm PLATE's description of the body; conspicuous dorsal and ventral sides, separated from each other by means of lateral planes "Seitenfläche", I have never seen. My conception is much more in accordance with the very small figures which GOSSE has given of the male. Near the anterior border below the wheel-organ are seen some hypodermal cells with conspicuous nuclei; I have been unable to detect a brain; eye and antennæ, dorsal as well as lateral antennæ seem to be absent. Most probably there exist two longitudinal muscles to withdraw the wheel-organ, but I have not ventured to draw them. The whole of the interior is filled by an enormous testis, almost reaching the wheel-organ and provided with two sorts of spermatozoa; laterally the testis is surrounded by two prostata glands, the size of which differs very much individually. At the posterior border there is a rather large opening, surrounded by a wreath of rather long cilia; it is the opening for the testis; as far as I can see, there is no real penis, but during copulation, and when the male whirls round the body of the female, the whole body as shown in fig. 4, is attenuated behind; in a peculiar amoeboid manner it is now drawn out into a cylindrical part which functions as penis. The testis is then pressed downwards and shows a similar prolongation to the body itself. A penis tube, ciliated on its interior walls, I have been unable to observe. Every sign of an alimentary canal and of excretory organs seems to be wholly lacking. The testis and prostata glands are surrounded by a greyish mass, in which are imbedded numerous often very large oil globules. The males swim with an almost incredible speed, and owing to their extremely small size, they are difficult to isolate and draw by means of camera.

### **Asplanchnadæ.**

Closely allied to the Notommatidæ through the two genera *Eosphora* and *Triphylus* the family comprises the three genera *Harringia* (= *Dinops*), *Asplanchnopus* and *Asplanchna*. The first-named genus has become best known through the excellent studies of DE BEAUCHAMP (1912 a, p. 223) and he being the first to show the connection with the *Notommatidæ* through the genera *Eosphora* and *Triphylus* (see especially

DE BEAUCHAMP 1909, p. 24—25). The males of *Harringia* are unknown, that of *Asplanchnopus* has been seen by PLATE and rather superficially studied by WEBER. The males of the genus *Asplanchna* belong to the oldest and best known of the Rotifera males.

### *Asplanchnopus myrmeleo* Ehrbg.

Male: Western 1888, p. 647.

Hudson Gosse, Suppl. p. 15. Pl. XXXII, fig. 13b.

Weber 1898, p. 384.

Plate 1886, p. 83.

WESTERN (1888, p. 647) has briefly described the male as follows:

The presumed male is found in a trough filled with water, where the female *A. myrmeleo* was then abundant. "It had the characteristic foot of the female. The brain is large, tripartite; an eye spot; two dorsal antennæ; a very large contractile vesicle, and numerous vibratile tags. There are the usual sperm-sack and protrusile penis, the latter lying behind the foot under a valve-like flap. — Size female:  $\frac{1}{25}$ , of male  $\frac{1}{50}$ ."

WEBER (1898, p. 384. Pl. 16, fig. 11) has observed the male only in one specimen. He only says:

"Il possède un repli membraneux, en forme de valvule, qui fait saillie en arrière du pied et protège le pénis. Le testicule et le pénis sont placés plutôt transversalement dans la cavité du corps et très en arrière." Size of female 960  $\mu$  à 1000; of male 460 à 500  $\mu$ .



*Asplanchnopus myrmeleo* ♂. after Weber.

PLATE (1886, p. 83) remarks:

"Von den bis jetzt noch nicht bekannten Männchen ist mir nur einmal ein halbtotes Tier zu Gesicht gekommen, das hinsichtlich der äusseren Gestalt so gut wie nichts erkennen liess. Der Hoden war dicht gefüllt mit runden Zellen, halbreifen Spermatozoen und jenen schmal-spindelförmigen unbeweglichen Körpern, die auch bei allen andern Männchen beobachtet sind. Ein Teil derselben flottierte frei umher, andere aber sassen mit ihrer Mitte den runden Zellen an, von denen sie daher offenbar gebildet werden."

It will be seen that the male may almost be regarded as unknown. For many years I have in vain searched for this form which, because of its intermediate stage between *Harringia* and *Asplanchna*, is of the greatest interest. Finally in the autumn of 1921 I found the animal in numerous little ponds, spread over a remarkable stone-covered heath in the middle of Seeland near Sorø (Rejstrup Oredrev). Only females with large yellow resting eggs were observed.

### *Asplanchna*.

A rather long series of *Asplanchna*-species have been described. The main forms are the following.

- |                               |                                  |
|-------------------------------|----------------------------------|
| <i>A. Ebbesbornii</i> Hudson. | <i>A. Girodi</i> de Guerne.      |
| - <i>Brightwelli</i> Gosse.   | - <i>Imhofi</i> de Guerne.       |
| - <i>priodonta</i> Gosse.     | - <i>Krameri</i> de Guerne.      |
| - <i>Sieboldi</i> Leydig.     | - <i>bowesii</i> Gosse.          |
| - <i>intermedia</i> Hudson.   | - <i>ceylonica</i> Daday.        |
| - <i>triophthalma</i> Daday.  | - <i>cincinnatiensis</i> Turner. |
| - <i>amphora</i> Hudson.      | - <i>hungarica</i> Daday.        |
| - <i>helvetica</i> Imhof.     | - <i>syringoides</i> Plate.      |
| - <i>Herrickii</i> de Guerne. | - <i>Silvestrii</i> .            |

Harring (1913, p. 15) has reduced the number to only 6.

- |                               |                            |
|-------------------------------|----------------------------|
| <i>A. Brightwelli</i> Gosse.  | <i>A. priodonta</i> Gosse. |
| - <i>Herrickii</i> de Guerne. | - <i>Sieboldii</i> Leydig. |
| - <i>intermedia</i> Hudson.   | - <i>Silvestrii</i> Daday. |

The species have been founded upon the structure of the jaws, number of eyes, form of ovarium, form of the body, form of the gastric glands, number of vibratile tags, and shell structure of resting egg. In his admirable studies on *A. amphora*, POWERS (1912, p. 441) has made it probable that the difference in numbers of vibratile tags are correlated with the general differences in the size of the organisms; further that in the same species (*A. Brightwelli*) we may find trophi with and without innertooth, and finally that the body-form in the same species undergoes the greatest variation. This is to be understood in this way that no single animal goes through all the various shapes; they are born with the shape they possess, and do not change it in their life time; but their progeny may have a shape, different from that of the parent.

It will be understood that nowadays it is a hazardous matter to found species upon the three characters: number of vibratile tags, the jaws, and the outer form of the body. As far as I can see, there is only a single good character, the shape of the ovarium, by means of which the genus may be divided into two groups, those with a round ovarium, and those with a horseshoe-shaped one. The main form for the first group is *A. priodonta* for the other *A. Brightwelli*; to the first group may further be referred *A. Herricki* de Guerne characterised by a peculiar glandular organ, near the urogenital opening. It has been well described by Wierzejski.

Most probably all *Asplanchna*-species with a horseshoe-shaped ovarium are subject to a greater or less polymorphism. To this group have been referred six species. *A. Brightwelli*, *A. amphora*, *A. Sieboldii*, *A. Silvestrii*, *A. intermedia* and *A. Ebbesbornii*. Of these species *A. Silvestrii* characterised by the double humped form of the female, well-described by ROUSSELET, has hitherto only been found in America and in brackish water; it seems to be a rather distinct species. *A. Sieboldi* Leyd. and *A. Ebbesbornii* Hudson are unquestionably synonyms. According to the descriptions it seems impossible to separate *A. intermedia* from *A. amphora* and provisionally *A. intermedia* may be regarded as a synonym for *A. amphora*. If this is correct, we



should only have four *Asplanchna*-species with a horse shoe-shaped ovarium *A. Brightwelli*, *A. Sieboldi*, *A. amphora* and *A. Silvestri*. With regard to *A. Brightwelli* it may be emphasised, that, even if there exist races of *A. Brightwelli* with inner tooth upon the rami (POWERS), this is commonly not the case. Undoubtedly in numerous localities there exists an *Asplanchna*-species with a horseshoe-shaped ovarium; it does not undergo any variation in form and the rami are always destitute of an inner tooth. At all events this is the case in Denmark. These species are referred to *A. Brightwelli*.

With regard to *A. Sieboldi* the polymorphism has been studied by v. DADAY (1888, p. 140) WIERZEYSKY (1893, p. 57) and LANGE (1911, p. 433), that of *A. Sylvestri* by ROUSSELET (1913, p. 57) that of *A. priodonta* especially by LANGHANS (1906, p. 439) and W.-L. (1908, p. 82) and that of *A. amphora* by POWERS. I for one confess that from the descriptions I am unable to distinguish *A. amphora* from *A. Sieboldi* but suppose that provisionally it is most correct to keep them distinct.

### *Asplanchna priodonta* Gosse.

Male: Gosse 1850, p. 18.

Hudson-Gosse 1889, p. 123.

Daday 1891, p. 79.

Weber 1898, p. 378.

Tab. V, fig. 6; Tab. VII, fig. 1; Tab. VI, fig. 6—7.

HUDSON-GOSSE (1889, p. 123, Pl. XII, fig. 2) describes the male as follows:

The male differs hardly at all in its internal structure from that of *A. Ebbesbornii*: though very different in shape. Its sperm-sack is supported by a strip of tissue that hangs from the head and resembles in shape and position the alimentary canal of the female. It is, however, imperforate and structureless and seems to have no other office than to support the sperm-sack and penis. The nervous ganglion unusually conspicuous. Two of its four diverging threads pass downwards to the dorso lateral rocket-headed antennæ, and two pass upwards to similar antennæ on the two apices of the corona. By slightly compressing a male, I put beyond question the fact that the contractile vesicle empties itself outward through the cloaca; for under slight pressure the vesicle contracted slowly, by stages as it were, collapsing partially in separate efforts instead of closing at once. As it did so, I distinctly saw, at each effort, the gradual passage of a plug of fluid down the cloaca, dilating its walls as it went. Size male: 200—400  $\mu$ , female 600—1000  $\mu$ .

The male of *A. priodonta* is most probably one of the most frequently observed and figured Rotifer males. Nevertheless, as far as I know, no better or more exhaustive description than that of GOSSE exists nor a better figure than that in HUDSON-GOSSE (compare f. i. this figure with DADAYS (1891: Tab. II, fig. 6—7, description p. 79) and the figure and description by WEBER (1898, p. 378).

It must only be added that MASIUS (1890, p. 651) without describing the male has given a good description and drawing of the male organs of *A. priodonta*. He gives the following very interesting observation hitherto unique and not corroborated by any other observer: "Tel est l'aspect ordinaire du canal déferent dont l'énorme diamètre semble peu en rapport avec ses fonctions. La raison du diamètre considérable de ce conduit s'explique par ce fait que (dans certains cas du moins) les spermatozoïdes sont rejetés à l'extérieur dans un volumineux spermatophore." MASIUS has observed the spermatophore three times and describes it as follows: "Il est sphérique ou légèrement allongé, jaune brunâtre et formé par la réunion d'un grand nombre d'éléments chitineux, polyédriques, de dimensions variables. Les plus grands

de ces éléments sont réunis aux environs de l'un des pôles; les éléments plus petits entourent le pôle opposé. La cavité du spermatophore est circulaire, mais excentriquement placée, de sorte qu'au niveau des éléments chitineux les plus petits, la paroi est aussi la plus mince. Le canal contenant un spermatophore a perdu son aspect glandulaire, le produit de sécrétion jaunâtre de ses cellules a disparu, il est probablement utilisé à la formation du spermatophore."

**Description:** The form of the male differs only very little from that of the female, but the head is not so conical, and the whole body somewhat narrower. The wheel-organ is a simple ring of cilia, surrounding the conical cone, it has no interruption dorsally or ventrally; at all events it is only very small. On the top of the conical disc there are two tufts of hairs; seen laterally, only one tuft is observed. I have not been able to detect prominences, carrying styli. The wreath is situated upon a ring of hypodermal cells. In the place where the mouth is in the female, is found a peculiar globular body, often provided with a prominence, formed like the beak of a parrot; to this globular body is fastened a long band, narrow in its anterior part, broader in the middle and narrower again near the testis, to the upper part of which it is fastened, and which it embraces. I am not quite sure, that this band is not hollow since it contains many globular bodies of different size which resemble oil globules, and which are not commonly found in any other part of the body. They are also indicated on the figures of HUDSON-GOSSE (Pl. XII, fig. 2c) and WEBER (1898, Tab. 16, fig. 8); a histological examination would indeed be very desirable. That the whole apparatus functions as a suspensor testis is in my opinion without doubt; on the other hand that morphologically it may be regarded as a rudiment of the alimentary canal is highly probable; the above-named globular body, lying where the mouth of the female is, may most probably best be regarded as a rudimentary mastax; like other rudimentary organs its stage of development undergoes large individual variation. The brain is mainly an elongate, large pear-shaped body, sending off forwards nerve threads to the cup-shaped disc and backwards threads to the two dorsal antennæ, situated before the middle of the body and two ventrally more behind; the heads are very broad, carrying on their blunt rounded outer ends long radiating setæ. On the underside of the brain is the large red eye; upon two prominences in the wheel-organ, two other somewhat smaller eye spots.

Of the longitudinal muscles we especially call attention to the two pairs of very strong muscles, running almost through the whole body; the two ventral ones are cleft near the corona and fastened to the above-named globular body; with the other end they are fastened to the cuticula, very near the testis and perhaps to this very same organ. The dorsal pair are fastened to the hypodermal cells of the corona and follow the intestinal band or suspensor testis, to which this is fastened; the other point of attachment is dorsally, almost in line with the first-named pair. These two powerful muscles draw in the wheel-organ. Near the middle of the body and near the two strong dorsal muscles is a point in which most of the other slighter muscles meet. At this point there are two long cleft muscles, which are fastened

dorsally to the hypodermal cells, further two parallel muscles which run ventrally aslope and are fastened with the other end near the globular body, the presumed rudimentary mastax; these muscles bend the forepart of the body and are able to give the corona a slanting position in relation to the axis of the body; further the muscles which run downward, one more dorsally and two more ventrally. Finally we find on the ventral side two pairs of rather narrow very long muscles, the one pair fastened with one end below the corona, with the other to the outer end of the ductus seminalis, the other pair with the cleft to the globular body, with the other to the opening for the urogenital canal. When this muscle is contracted, the whole posterior part of the body is bent downwards and forwards. Simultaneously with this, the muscles which are fastened to the opening of the penis, are loosened and, partly by means of augmented pressure in the body cavity and the numerous muscle threads in the cuticula, the testis is pressed downwards out into the urogenital canal. Transversally over the body are stretched some transversal muscle bands, running between the dorsal and ventral muscle system. A closer examination will further show a system of extremely fine muscle threads which mainly form a very wide-meshed net-work, directly under the cuticula; where these threads meet each other, we find a granular protoplasmatic structure, in which often a nucleus is seen: this net-work is most developed in the hind part of the body; where the threads meet each other, long, extremely fine, threads run downwards, mainly from the wheel-organ; if we observe a living *Asplanchna*, we shall see that it very often alters its form; now this now that part of the cuticula is drawn in and on the smooth surface of the body a larger or smaller hollow may be shown: this power of altering its form comes from the muscle network; if two specimens are compared, it will be seen, that it is never developed in quite the same manner.

As far as I have been able to see, in *A. priodonta* just as in the other specimens here mentioned, we find two sorts of lateral canals in the excretory organ on both sides of the body. The one may be described as a curved ribbon with strong curves and knots; they are tubes of a loose granular substance, with clear nuclei imbedded in their walls: at the sides of these tubes are the other sort; these canals are straighter, narrower and their lumen is more hyaline; they carry four vibratile tags; as far as I have seen, neither more nor less.

The real connection between the two canals I have not been able to see. With regard to the finer structure of the organ in the female I refer the reader to the excellent paper of WILLEM (1910, p. 21). The canals debouch into the contractile vesicle, which is very large; over its surface run a number of very fine muscle threads meeting each other almost in the centre of the bladder; it opens in the urogenital canal, very near the opening of the penis. To this point are further attached two small, short muscles, fastened with the other end to the bladder. The testis is rather small, pyriform, containing the two sorts of spermatozoa and opening in a urogenital canal. When used under the mating process, the urogenital canal



is forced outward, the whole hind part of the body is curved and the urogenital canal is now in two tempi, figured in figgs. 6—7, forced outwards and turned inside out; in this case it is altered into a hyaline cup traversed by the ductus seminalis and furnished at its base with a wreath of fine not vibrating cilia. In this position at the moment when the sperma is to be thrown over into the female, the testis has altered its form, now being much more slender and more longitudinally stretched. If the animal is held in this position by means of pressure, we see the bladder slowly fill itself; it cannot be emptied, and as the figure shows, it has now a constriction in its lower part. The short ureter and its opening in the urogenital canal is now very conspicuous; the canal in its outer part is covered with short cilia. Sometimes I think I have seen a series of parallel transversal stripes as indicated in the figure in this shape of the bladder.

I may add that the variation in form and size of *A. priodonta*, so characteristic in the female (LANGHANS 1905, p. 171; 1906, p. 439; W.-L. 1908, p. 82), has not been observed in the male sex.

#### A. Brightwelli Gosse.

- Male: Brightwell 1848, p. 153.  
 Dalrymple 1849, p. 340.  
 Hudson-Gosse 1888, p. 122.  
 Rousselet 1901, p. 1.  
 Daday 1891, p. 84.  
 Tab. VII, fig. 2.

DALRYMPLE (1849, p. 340, Tab. 34, fig. 11—14) has described the male; in the following the description is given in somewhat abbreviated form.

The male is about three-fifths the size of the female, generally resembling in shape, but more flattened at the lower part or fundus, and more prolonged at the side, corresponding to the vaginal opening in the female, and which in the male presents a similar valvular opening though comparatively smaller in extent. Within this valve is observed a short canal, leading to a large spherical bag which may be distinctly seen, filled with molecular bodies in constant tremulous motion. From this body (the sperm-sack) a short but thick rounded body projects into the canal, before mentioned as leading to the lateral opening; around the extremity of this projecting process, and even within it to a short distance, is a visible ciliary motion, indicating a canal. The whole organ is regarded as a penis; a very exhaustive description is given of the muscles which draw in and out the presumed penis. Lateral canals, vibratile tags and contractile vesicle as in the female, but there are no mandibles, pharynx, oesophagus, pancreatic glands or stomach; globular masses in the body cavity; they are to be regarded as rudiments of the stomach.

HUDSON-GOSSE (1889, p. 122, Pl. XII, fig. 1 c) gives a figure of the male but hardly any description.

ROUSSELET (1901, p. 1) only remarks that the male is without a hump.

DADAY (1891, p. 84) only says: „Körper cylindrisch, oval, hinten etwas abgestutzt, ohne Fortsätze. Grösse 300—500  $\mu$ .“

**Description.** The male in many respects differs very conspicuously from the male of *A. priodonta*. It is much more globular, almost isodiametric, still somewhat

attenuated in front. It is extremely hyaline; very often I have found specimens which, in contracted form, show a tendency to make lateral humps; when swimming, they always disappear. The wheel-organ is constructed just as in *A. priodonta* and so also is most probably the coronal disc, but owing to the slight material, I am not quite sure upon this point. The most peculiar structure in the anatomy of the species is that the long intestinal band, to which the testis is fastened in *A. priodonta*, is totally lacking here; the result hereof is that, whereas the testis in *A. priodonta* lies almost in the longitudinal axis of the body, in *A. Brightwelli* it lies almost transversally. Remains of the alimentary canal are totally absent in this species. The brain and the two pairs of antennæ are constructed in accordance with that of *A. priodonta*, but there is only a single eye lying upon the underside of the brain; not two eyes in the ciliary wreath. The muscles are mainly in accordance with those of *A. priodonta*. There are the same two pairs of strong longitudinal muscles, hauling in the wheel-organ: the ventral pair is deeply cleft posteriorly, embracing with its two parts the testis which is kept in place mainly by these muscles; very conspicuous also are the much narrower muscles dorsally and ventrally, which take the same position and have the same significance as in *A. priodonta*. A little behind the middle we find the same spot dorsally as in this species, to which two longitudinal as well as two slanting muscles with two other pairs running parallel, are fastened; to the same point is further attached the downward directed muscle which with its other end is fastened to the opening of the testis in the urogenital canal. Almost to the same spots are also fastened two small muscles to the contractile vesicle. Apart from the number of vibratile tags which, in this sex as in the female, is greater (about 10) than in *A. priodonta*, I cannot find any difference with regard to the excretory organ. The contractile vesicle may be very large. There is the same wide meshed system of extremely fine threads under the cuticle; it seems, as if one of the turning points in this system is just the point where the above-named many stronger muscles meet. I have often observed that at the same moment when these muscles are contracted, all the fine muscle threads are simultaneously contracted, and the whole form of the posterior part of the body altered. Below the corona is a series of small parallel muscle bands. The testis is almost globular; in the ductus seminalis, and in the urogenital canal I find no differences from *A. priodonta*. In the testis are found the two sorts of spermatozoa. It is rather peculiar that, whereas *A. priodonta* at the first glance is distinguishable from almost all other *Asplanchna*-species, owing to the globular ovary, the ovary being horseshoe-shaped in most of the others, the testis in all species has quite the same globular form.

It may further be added that, on the dorsal side of the animal we almost always find some globular masses of very different size, form, and number. In my opinion we have here rudiments of yolkmasses, in some way of nutrimental use to the animal: they diminish during growth. They are mentioned by DALRYMPLE and are indicated in the figure of Hudson-Gosse (1889, Pl. XII, fig. 1 c). Size: male 166—200  $\mu$ , of female 500—1500  $\mu$ .

Curiously enough it seems that the male has only been found a few times after it has been observed by BRIGHTWELL and DALRYMLPE; it is figured by HUDSON-GOSSE 1889, Pl. XII, Pl. 1 c, but no new observations are added to the old ones.

***Asplanchna Sieboldi* Leydig.**

Male: Leydig (1855, p. 30).

Hudson-Gosse (1889, p. 121).

Daday (1891, p. 87).

Tab. VII, fig. 3.

LEYDIG (1855, p. 30, Tab. II, fig. 12—14) has given an excellent description and very good drawings of the male.

The form differs from that of the female, not being campanulate but cone-shaped, with two pairs of humps, one pair larger; almost in the middle of the body, and one pair nearer to the corona; during the swimming motion the arms are stretched out and drawn in. The wheel-organ is in full accordance with that of the female, the coronal disc carrying the same elevations with stiff setæ and bunches of bristles as this sex; the brain gives off nerves to the elevations with the setæ on the disc and to the ventral lateral antennæ; the dorsal pair is not mentioned. No alimentary canal; the excretory organ in full accordance with that of the female (vibratile tags about 50). The large testis pear-shaped; ductus seminalis in its interior covered with cilia and provided with prostata glands; the structure of the spermatozoa is thoroughly described. Muscular system in accordance with that of the female, strong longitudinal muscles and fine transversal bands, of which one pair are used to draw in the humps; on the base of the humps they appear "sternförmig", sending off fine threads to the periphery. In the body cavity behind the great humps cell material which LEYDIG regards as stored nutriment deriving from embryo. LEYDIG's drawings were subsequently reproduced by TOTH (1861, p. 178, Tab. II, fig. 13—14).

HUDSON-GOSSE (1889, p. 121, Pl. XI, fig. 3) have given a very good description and drawing of the male as *Asplanchna ebbesborni*.

It must especially be pointed out that H.-G. have observed the rounded masses adhering to the dorsal surface, just below the humps. They are in accordance with LEYDIG but with some doubt, regarded as "a kind of stored-up material to compensate for the male's inability to take nourishment". The muscle system of the penis and testis is well described and so also especially the excretory system with the flocculent ribbons, the tubes and the large number of vibratile tags (about forty on either side).

DADAY (1891, p. 87) gives a very insufficient drawing of the female and describes it shortly as follows:

"Körper vorn cylindrish, mit zwei bauchständigen Anhängen, hinten conisch, mit zwei kräftigen Seitenanhängen; — mit einem einzigen Stirnauge." Size 200—400  $\mu$ , female 800—1500  $\mu$ .

Description. Form of the body not bellshaped as in the female, but conical as indicated by LEYDIG. It is provided with two sleeve-like prolongations, situated almost in the middle of the body; of the two others placed nearer the wheel-organ and indicated by LEYDIG and HUDSON-GOSSE I have only seen slight vestiges. The prolongations may be drawn in and out during the swimming motion; they are always empty; the whole animal extremely hyaline.



The coronal disc is conical with two apices. The ciliary wreath is a simple ring of cilia, as far as I have been able to see without any interruption either dorsally or ventrally. The brain is large, flattened; when the animal, as the figure shows, is seen laterally, pear-shaped. On the coronal disc are found two hairtufts, and each of these receives nerves from the brain; four long nerves, two ventrally and two dorsally, run down to the two pairs of antennæ; there is only one red eye and no eye spots in the corona. As in *A. Brightwelli* it is not possible to point out the slightest trace of an intestinal band; the testis is only fastened by muscles, and here also has an almost transversal position.

With regard to the muscular system it will be seen by comparison with the figures of *A. priodonta* and *A. Brightwelli* that especially with regard to the great retractors of the wheel-organ, the slanting transversal muscles, and some of the muscles to the penis, there is a great resemblance in all three species. There is only this difference, that ventrally we find a rather large muscle, fastened upon the testis and running up to the wheel-organ; this muscle has no congruent in the two other species. Peculiar too is the much coarser equipment of fine muscle threads below the cuticle; further that these threads almost run parallel and are especially developed in the hind part of the body; it is on this system of cuticular muscles that the almost incredible variation in outer form in the first line depends. In specimens, deriving from the locality where the species was first found, a very little duck pond belonging to a little farm a few kilom. from Hillerød, this system of muscle threads was very conspicuous: this was also the case with the specimens deriving from the duck pond in the little village of Fjenneslev near Sorø. In the vascular system two sorts of canals are distinguished, the one very large and long forming windings and slings, the other more straight carrying in a long row at all events more than thirty vibratile tags and perhaps more. LEYDIG (1855, p. 27) mentions about 50, HUDSON-GOSSE often more than forty (1889, p. 122). The contractile vesicle when fully distended, occupies a very large part of the body cavity; it is covered with a conspicuous muscular network, the muscle threads meeting each other in two opposite points.

The testis is pear-shaped and very like that of *A. Brightwelli*; it is as always in the Asplanchnas rather small in comparison with the size of the animal. The ductus seminalis and urogenital canal are formed quite as in the other species; on the sides of the canal are a series of glands which may be regarded as prostata glands; similar ones I think I have seen in *A. Brightwelli*, but not so conspicuous as here.

Especially in the middle of the body and near the sleeve-like prolongations but also otherwise we find peculiar irregular bodies also mentioned by LEYDIG. He is of opinion "dass diese Masse ein Rudiment des Zellenmaterials ist, welches beim Embryo zum Aufbau des Magens bestimmt wird, aber da einmal die Männchen ohne Nahrungskanal sein sollen, nicht zum Verbrauch kommt". I agree with LEYDIG in the first part of this sentence, but am not quite sure that this store nutriment is of no significance for the animal. Size of male 250—300  $\mu$ , of female 600—1000  $\mu$ .

*A. Sieboldi* (= *A. Ebbesborni*) seems to be a very rare animal in our country.

I saw it more than 25 years ago; it was found in the above-named little duck pond lying very near the birth place of my good friend, the celebrated Danish Naturalist Dr. TH. MORTENSEN. The drawing derives from these specimens. Later on I never found the animals in this little pond, and when I explored the pond again in 1921, I found it quite altered and with hardly any Rotifers in it at all. I have been in search of the animal during all these years; not till 10/VIII 1921 did I find it again in another duck pond in the little village of Fjenneslev near Sorø. I had the good fortune to come across it in the sexual period and got several males. In the samples were only humped females and males, but it was in the last part of the sexual period, the pond being almost dried up. In 1922 I never succeeded in finding the species again.

I am not quite sure that my determination is quite right. The species being equipped with large humps, well developed in all the many females and in the males which I have seen, but really often withdrawn when swimming, it is impossible to refer it to *A. Brightwelli*. Equipped with one single eye, conspicuous humps and horse-shoe-shaped ovarium the animal must be referred to the group *A. intermedia*, *amphora* and *Sieboldi*. As the jaws have a large innertooth and as there are more than thirty vibratile tags, it cannot be referred to *intermedia*, a species which in my opinion is rather doubtful. *A. amphora* is really a proteus among the *Asplanchna* species; only if a population from a pond were observed the whole year round, would it be possible with certainty to determine *A. amphora* from the other species; as however I never found the campanulate and saccate forms, characteristic of *A. amphora* in the colonies from Frerslev and Fjenneslev, and the first-named colony was observed four times in the course of two months (May—June), I do not think it can be correct to refer these populations to *A. amphora*. Comparing my material with the long descriptions of HUDSON-GOSSE and LEYDIG I find great conformity upon all essential points; I only lack the two humps upon the neck below the wheel-organ but as even these humps are subject to great variation I cannot see that it would be impossible, only because of that, to refer my specimen to this form.

It was in this species that DADAY (1889, p. 140) observed the polymorphism of the *Asplanchnadae*. He found two different forms of females, partly saccate, partly humped; both forms are able to produce partly females of their own form, partly those of others, partly males and, after fertilization, resting eggs. I then found a peculiar species in North Seeland; it was in May, and in the pond only the humped form existed which, during swimming, had very often drawn in the humps. I therefore supposed, (1898, p. 200) that there really only existed one form with great power of altering the shape of the body. At that time I did not know WIERZEJSKI's paper (1893a, p. 57); he too had observed the phenomenon and interpreted it in accordance with v. DADAY. In 1911 LANGE (p. 433) found an *Asplanchna* at Schönaun near Leipzig. By studies in cultures, he showed that the females deriving from resting eggs were always of the saccate form, and that the humped form did not arrive before the third generation. The appearance was quite sudden. From his own observations on *A. amphora* POWERS (1912, p. 536) concluded

that my statement that the two forms could not be distinguished from each other, was wrong. From the combined investigations of WIERZEJSKI, LANGE and POWERS, I am sure that I have been wrong in my supposition. The chief reason for that was, that in my pond, I did not at that period see any of the saccate forms, and secondly, that v. DADAY had not mentioned that the humped forms, when the humps were drawn in, were indistinguishable from the saccate ones.

I regret very much that I have not been able to find the species again in time and so complete my observations. When (<sup>10</sup>/<sub>8</sub> 1920) I found the new locality (Fjenneslev) it was most probably too late in the year to get the saccate form, and the pond was so far away from my laboratory that regular proofs could not be obtained.

***Asplanchna intermedia* Hudson.**

Male: Hudson-Gosse. Supp. 1889, p. 12.

Rousselet 1901a, p. 9.

Daday 1891, p. 87.

HUDSON-GOSSE (Supp. 1889, p. 12, Pl. XXXII, fig. 15).

"The contractile vesicle and sperm-sac of the male are very small; and the lateral canals have the vibratile tags arranged in a straight line on either side. The creature is so wonderfully transparent and empty that it is difficult to see... The hind dorsal corner of the body is somewhat prolonged into a sort of third hump, and darts out stiff and obvious (as do the lateral arms) when the head is retracted. The opposite ventral corner is prolonged to a blunt point, and is the sheath of a long protrusile penis. What appears to be an atrophied oesophagus and stomach hangs freely in the body-cavity, between the head and the above-named dorsal hump. In one specimen I saw tags in which no ciliary motion was visible. Length m.  $\frac{1}{80}$  i."

ROUSSELET (1901a, p. 9, Pl. I, fig. 2).

The males of *A. intermedia* and *A. amphora* resemble each other very much; both have two humps, projecting laterally on the sides of the body, only the male of *A. intermedia* is much smaller than that of *A. amphora*.

v. DADAY (1891, p. 87) only says:

"Körper conisch, mit zwei Seiten- und einem Rückenanhäng; mit einem einzigen Stirnauge."

***Asplanchna amphora* Hudson.**

Male: Hudson 1889 Supp. p. 13.

Powers 1912, p. 441.

Western 1890, p. 65.

Daday 1891, p. 85.

Tab. VII, fig. 4.

WESTERN (1890, p. 65) remarks that he has observed

that as the females grow larger and older the lateral humps almost, if not entirely, disappear. Among these large apparently humpless females he has however found two large humpless females with young ones in utero, which were undoubtedly of the humped variety. He has



also seen the humped males in utero. He has further observed that *A. amphora* may entirely disappear from the pond, whereupon *A. Brightwellii* turned up in great abundance.

DADAY (1891, p. 85) only says: "Körper conisch mit zwei Seitenfortsätzen."

**Description.** Body form very peculiar; almost triangular with circular top, a triangular base, a broad dorsal side and rather narrow rounded ventral side; on each of the two side-planes are two sleeve-like prolongations, two humps of the cuticle; they differ in size and form from specimen to specimen, are not equally developed at all times of the year, and have never quite the same appearance in different ponds; they are often drawn in during the swimming motion and can suddenly be unfolded; this always takes place, when the wheel-organ is withdrawn or when the swimming direction is altered. They are always destitute of inner organs. The whole animal is extremely hyaline, crystalline. I have never found more than two humps. The coronal disc is conical with two apices. The ciliary wreath is a simple ring of cilia, as far as I have been able to see, without any interruption dorsally or ventrally. The brain is large, flattened, much broader than long, indistinctly divided into two parts, and sending nerves off from the corners to the coronal disc and to the body behind. On the coronal disc are found four hairtufts, each of these receive nerves, as shown in the figure of the animal, seen dorsally. There is only one red eye; no eye-spots in the corona; four long nerves, two ventrally and two dorsally run down to the lateral antennæ. Seen from the dorsal or ventral side, a long cylindric rather narrow faintly curved body is seen, hanging down from the corona; during swimming the organ is seen dangling hither and thither; it differs in size and development from specimen to specimen; it has hitherto only be observed in *A. intermedia* by HUDSON. Like this author I regard it as a rudiment of the alimentary canal; at all events it does not reach the testis which, just as in *A. Brightwelli*, is free and has no intestinal band connecting it with the wheel-organ. The muscle system is, especially in this form, very conspicuous, on the other hand owing to the peculiar form of the animal difficult to study. Seen dorsally *A. amphora* exhibits some remarkable differences in the course of the great retractors of the wheel-organ. As in the other species they really run from wheel-organ to testis, but, if I am not mistaken, before they reach the wheel-organ, they cross each other in a rather peculiar manner (see Tab. VII, fig. 4), perhaps this is a peculiarity in some individuals or in the whole population investigated. Seen laterally it may be shown that the other muscles dorsally and ventrally as well as those to the testis, are in full accordance with those of *A. priodonta* and *A. Brightwelli*; the special muscle from corona to testis in *A. Sieboldi* I have not found here. Of peculiar interest are the four very conspicuous transversal muscles, one of which crosses the body on a level with the humps, dissolving themselves into three or four very fine threads, fastened to the cuticula of the humps. After these four more conspicuous bands, one or two other very fine threads, parallel with the others, are visible. The whole body, especially in the hind part, has a very conspicuous wide-meshed network of fine threads, running below the cuticula.

The almost incredible formshifting power of the animal depends chiefly upon the muscle system. The excretory system exhibits a series of peculiar anatomical structures. The canals are not to such a high degree curled up, as is the case especially with *A. priodonta*. On each side of the body run three canals, the two of the structure indicated by HUDSON-GOSSE as tubes of loose granular stuff; the third one is somewhat clearer, perhaps with more solid walls, bearing about forty and often fifty vibratile tags; this canal has a peculiar cul de sac appendix, running down in the vicinity of the dorsal antennæ. How these three canals are connected with each other I do not know with certainty; in their whole course they are almost free of each other, only meeting near the corona and the bladder. This, when fully distended, may be extremely large, filling up a great part of the body cavity. The testis is rather small; the structure of the ductus seminalis and urogenital canal with the opening of the vesicle just at the boundary between both is in accordance with the facts found in the other three species. Dorsally round the testis there is deposited stored nutriment in the shape of yolkmass in different amounts. — Size of a male 500  $\mu$ , of female 1500—2000  $\mu$ .

This very peculiar Rotifer I have only met with in a single pond, extremely shallow, rich in organic matter; as it was found, the pond two months before had just been dried out; before, it was almost overgrown with vegetation, and the water a frumenty, overfilled with green algæ.

It was in the last part of August that the first sample was taken, and till the middle of October the pond was visited every week. The first time I found this Rotifer, I immediately saw that I had found a population of an *Asplanchna* which corresponded with those colonies which were found by POWERS. In the following I shall try to give an extract of his paper.

*A. amphora* was living in vile pools on the alkaline flat west of the city of Lincoln, Nebraska. The water was here dark brown with alkali and the essence of compost. It was shown that the culture only thrived well where the "water" had the original composition of the native home of the animals. In nature, every rain-shower which diluted to an appreciable extent the vile ponds in which this *Asplanchna* flourished, resulted in the death of the entire stock, which was only replaced by the hatching of new individuals from resting eggs. The main result of the studies of POWERS was, that *A. amphora* was a trimorphic species divided into three different forms: the saccate, the humped and the campanulate form. The first (A) was invariably produced from resting eggs, multiplying by rapid parthenogenesis through several generations. It always preponderated in the beginning of the year, but was then rarer and rarer. It was succeeded by the humped form (B), originating from the former by rapid saltation; it produced chiefly its own type; the size of the humps may differ very much according to nourishment. Owing to cannibalism then a third form (C) arose, the campanulate type, which reproduced both its own form and B. The three forms differ from each other in the following main points: in A the corona is about equal to the diameter of the body; and nearly circular in outline; there are no humps;

the number of flame cells vary from 20—40, the contractile vesicle is large; trophi are constructed as in the next form but somewhat smaller (95—135  $\mu$  long). Length of entire animal 500—1200  $\mu$ .

In B. the corona is oval; the flame cells 40—60. The contractile vesicle small; trophi strong 130—200  $\mu$  mainly 150—170  $\mu$ , enclosing, when closed, an area which is not oval, but widest in its distal third, with prominent tooth projecting inward, delicate lamellate teeth near the tips, and the two rami interlocking, when closed, by means of one bifid and one pointed tip. Length 1000 to 1800  $\mu$ .

In C the body is very broadly saccate to broadly campanulate with very heavy walls and muscles strongly flattened dorso-ventrally, never with humps; corona oval and very broad, its breadth frequently equalling the length of the animal; coronal disc concave, instead of convex; flame cells 80—115, contractile vesicle small; trophi 300—340  $\mu$ , very large, enclosing a narrowly oval area; inner teeth comparatively less prominent than in preceding types, set at an acute angle with the ramus, and more firmly fused with it than in the preceding types; lamellate teeth near tips of rami much developed and meeting with cutting edges in middle line; tips of rami not interlocking, but shearing past each other when closed. Length of entire animal approximately 1800 to 2500  $\mu$ .

It was further shown that intermediate stages were commonly rare, and that the three forms were standing sharply against each other; they were not all to be found in the same sample, and all three forms were not necessarily developed in all the small localities, where the species was examined.

There are also other differences to point out in the three forms, especially with regard to propagation; the saccate form which most probably is the only one which develops from the resting egg, is usually crowded with embryos, nine or more; the humped form as a rule contains only one single young one and the campanulate form contains a few; by means of degeneration in cultures the saccate form may derive from the humped one, but this is an exception. The campanulate forms make their appearance within at most a week. Sometimes a single individual, either young or fully developed, would first be discovered. In every instance the sudden appearance of the campanulate form was followed by its very rapid multiplication, coincident with a still more rapid diminution in numbers of the humped form. The latter were eaten up by the former. Campanulate forms were also reared in the cultures by using the young *Moinas* as food, and a pond was discovered where the natural appearance of *Moina* caused an enormous production of campanulate forms, even directly from saccate ones, without humped ones as an intermediate stage. The entire population of a teeming *Asplanchna*-pond readily changes from the saccate to the humped type in one week; the saccate forms giving rise to the humped ones in the first generation, almost of the same size as the mothers. The next generation gives large-sized, typical humped individuals; later on the campanulate form appear among them with the utmost abruptness owing to cannibalism. Between the alterations in the colonies, when they pass from one form into another, transitional periods appear; in these



the colonies have an almost incredibly chaotic appearance, but commonly the transitional periods are brief. Unfavourable conditions prolong these periods. POWERS could further show that exhaustive nutriment, for instance copious feeding with *Moina*, not only gave rise to the campanulate form, but also the humped forms, deriving from it, which possessed very long, highly developed humps that may be so long that they exceed the animal's length. It is supposed that each of the minor fluctuations which the three forms of the species undergo, will almost certainly resolve themselves into factors of nutrition.

POWERS has pointed out the very essential fact that the above-named three forms are all able to produce males, and that these males all have the same appearance; they are produced copiously by the humped and campanulate types, rarely and only in distinct periods by the saccate type; the size of the males varies greatly, from 300 to 1500  $\mu$ . Also the resting eggs are produced by all three forms, rarely by the saccate; in the humped three to six, rarely nine, are seen; in the campanulate also a high number.

It will be understood that the saccate form in almost all respects is very near to *A. Brightwelli*. The main difference between *A. amphora* and *A. Brightwelli* is that the trophi of the lastnamed species invariably lack the large inner tooth, whereas it is always well developed in all three forms of *A. amphora*. POWERS has however found a population of *A. Brightwelli*, where the trophi bore a strong inner tooth in the exact position in which this is found in *A. amphora*. He has further shown, that parallel cultures with identical conditions as to food and temperature, the one with the saccate forms of *A. amphora*, the other with the typical *A. Brightwelli*, invariably gave the same results; the saccate forms gave the humped forms; *A. Brightwelli* always *A. Brightwelli*; further that cultures of *A. Brightwelli* with inner tooth, continued over 6 weeks, invariably only gave the same type. He therefore concludes, that *A. amphora* and *Brightwelli* are really distinct species, and that there may be found special races also in *Brightwelli*.

The colony which I found in August in the above-named little pond contained the species in enormous masses. The main form was the above described humped one, but among them were numerous giants of the campanulate form, often measuring about 2000  $\mu$ ; a very few specimens of the saccate form occurred; only the two first-named forms produced males; these were always humped. As far as I know, this is the first time after POWER's investigations that the species with all its three forms was found. The campanulate form fed upon the humped form and upon the young ones of *Daphnia*. In September resting eggs appeared in the humped and the campanulate form. In the last part of October the males disappeared, the humped ones became rarer and rarer, and in the first days of November only a few very large campanulate forms remained. By 15/XI *Asplanchna* was found no more. In December we had a short frost period; the pond thawed again and was finally frozen about 6/I 22. The very interesting discovery occurred at a moment when I was very much occupied with studies relating to other Rotifers, and I was unable to pay as much attention to the colony

as I should have wished. A more thorough investigation was planned for the year 1922, and on  $5/5$  1922 shortly after the pond had thawed, the first sample was taken. The whole year round every ten days samples were taken, and I was prepared for a more thorough investigation. On 5/V the first females appeared; they were, as expected, of the saccate form, but not to be distinguished from a typical *A. Brightwelli*, the rami being without inner tooth. The species was observed during the whole of May and June; it was rather rare, and no humped forms appeared. Then a period of heavy showers occurred, and during the whole time from July to late in August the downpour was extremely high; the temperature was low not above 14—16° C. In the last part of June the species disappeared. The pond was under regular observation till 29/I when the frost appeared, and the pond was frozen over. During this time not a single *Asplanchna* was observed in the pond. Most probably the melancholy result of so many excursions was due to the bad weather. In 1921 the whole summer was very dry, the temperature was above twenty degrees Celsius, and often rose to twenty-five; the downpour was extremely small. Whereas in 1921 the pond teemed with flagellates, often forming scum upon the surface, it was brown in 1922; of flagellates appeared only *Eudorina* and later on *Volvox* both in relatively few numbers. The pond will be under regular observation also in 1923.

### ***Asplanchna triophthalma* Daday.**

Male: Daday 1883, p. 261.

v. DADAY (1883, p. 261, Tab. fig. 3) gives a long description of the male unfortunately in Hungarian.

It is furnished with a figure, which in a very high degree differs from all other figures of the males of *Asplanchnadæ*. It is much more in accordance with the males of *Brachionus*; this holds good especially with regard to the structure of the testis and penis. The three eyes which are stated to be one of the most characteristic peculiarities in the specimen are indicated in the figure.

v. DADAY (91, p. 84) only says: Körper cylindrisch, nach hinten verengt, ohne Fortsätze; mit zwei Seitenaugen und einem Stirnauge. Size male 200  $\mu$ —400  $\mu$ ; female 800—1200  $\mu$ .

### ***Asplanchna Sylvestrii* Daday.**

Male: Rousselet 1913, p. 61.

ROUSSELET (1913, p. 61, Pl. 5, fig. 5—6) gives the following short description.

*A. Sylvestrii* is mainly characterized by the double-humped form of the female. ROUSSELET (p. 62) shortly states "that the male is humped but the side humps are not bifid. According to the description it is indistinguishable from the male of *A. amphora*. Length of female 1150  $\mu$ . of male 408  $\mu$ . The species is described by DADAY (1902) from Chile, and later on found in Devil's Lake, North Dakota; the water is brackish."

### **General remarks.**

The males of the genus *Asplanchna* are very little reduced; apart from the reduction of the alimentary canal they are almost constructed quite like the females.

They belong to the largest known Rotifer males, reaching about  $500\ \mu$ ; as far as we know, they never present variation in outer form; they are not polymorphic, and if they belong to species where females in one of their forms are humped, they are always humped.

The wheel-organ and disc differ but little from those of the female; the alimentary canal is always rudimentary, best developed as suspensor testis with a rudiment of a mastax in *A. priodonta*; very short in *A. amphora* and totally absent in *A. Brighwelli* and *A. Sieboldi*; in these species the testis is only supported by strong muscles. The nerve system is constructed in accordance with that of the female, and so are the different sensitive organs. This is also the case with the excretory organ; the number of vibratile tags correspond with those of the female, and a large contractile vesicle is always present. There is great coincidence with regard to the muscle system, peculiar is the great development of fine muscle threads below the cuticula. Whether the ovary is horseshoe-shaped or globular in the female, the testis is always globular; there is no real penis, the ductus seminalis opens into a canal in which also the canal for the contractile vesicle opens; during the copulatory act the ductus seminalis is pushed forwards, turned inside out and used as penis; it has a wreath of cilia.

Almost all observers have seen some globular bodies different in size and number, lying in different parts of the body. They are commonly (LEYDIG, HUDSON) regarded as stored nutriment for the males, which have no possibility of getting food; they derive from yolk masses, which the embryo has not used. LANGE (1911, p. 439) has shown that this supposition is correct. He says as follows: "1910 züchtete ich *A. Brighwelli* und habe dabei ein ♂ 7 Tage lang lebendig erhalten. Die darauffolgende Untersuchung des Zellhaufens ergab, dass er sich während dieser Zeit fast völlig aufgezehrt hatte. Auch für *A. Sieboldii* habe ich in allen Fällen nach 1—2 Tagen eine starke Abnahme in den Flächenausdehnung und Dicke des dorsalen Zellenkomplexes konstatiert." I can further remark as follows. The *Asplanchna* males most probably belong to those with the greatest longevity. POWERS has kept them alive for 2—4 days (1912, p. 534). LANGE for 7. I myself for 4. I have isolated males, whose birth I have observed; they had, at birth, a size of about  $300\ \mu$ , when they died four days later, the size was about  $400\ \mu$ . At birth there was a great deal of store nutriment, at death it had disappeared; growth after birth has hitherto not been observed in Rotifer males.

### Rattulidæ.

The family comprises the two genera *Diurella* and *Rattulus*. The males in this family have hitherto been quite unknown. Characteristically enough, JENNINGS, in his excellent monograph of the family (1903 a, p. 273), does not mention the males with a single word.

The males of the genus *Diurella* are still unknown; of the genus *Rattulus* I have found the males of three species.



**Rattulus stylatus** (Gosse).

Tab. III, fig. 5.

**Description.** Body pearshaped, rather soft with thin hyaline cuticula, presenting three rather well-marked transversal lines; wheel-organ a terminally situated disc, surrounded by a wreath of rather short cilia; the disc itself covered with short hairs, in the middle a tuft of long, strongly developed hairs. No antennae observed. A brain with a large red irregular eye-spot. The whole body cavity filled with a greyish mass, containing numerous oil-globules. In this mass a very large almost globular testis, reaching up before the eye; two sorts of spermatozoa; the testis opens into a peculiar chitinized penis-tube which ends in a disc with the opening of the penis in the middle of the disc; the penistube can be withdrawn and again protruded. I have been unable to find any remains of an alimentary canal, of excretory organ, retrocerebral organ, antennae, prostata or even muscles in the male; I suppose that the muscles, at all events, may have been present. Size of male 60  $\mu$ , of female 140—180  $\mu$ .

In one of my experimental ponds near Hillerød *R. stylatus* is very common; it has a large maximum in May; when I had isolated from the lighted border of the vessel many hundred females, the males appeared. The eggs were laid on the bottom, and the extremely small and extremely rapid males appeared.

**Rattulus pusillus** (Lauterborn.)

Tab. III, fig. 6.

**Description.** Body pyriform, hyaline with a rather soft cuticula furnished in front with a peculiar system of longitudinal folds, by means of which the cuticula can be folded over the wheel-organ, when this is drawn in; at the posterior end an inconspicuous cleft; a wheel-organ which can be placed vertically on the longitudinal axis and be bent slightly ventrally. It consists of a wreath of short cilia, surrounding a cilia-covered disc with a protuberance bearing a tuft of cilia. The brain is very large, sending two nerves to a little dorsal antennal organ; a large red eye is situated on the underside. Testis large, globular with two prostata glands; the penis chitinized, somewhat curved, ending again in a somewhat hollowed circular disc with a central opening; two sorts of spermatozoa. No trace of alimentary canal, excretory organ, or retrocerebral organ; lateral antennae have been observed; four very conspicuous transversal muscle bands, but no longitudinal muscles have been seen. Size of male 60  $\mu$ , of female 115  $\mu$ .

*R. pusillus* was found common on 3/VIII 1921 in a pond near Sorø; of other Rotifers there were only *Anuraea hypelasma* and *Synchaeta oblonga* in the sample. Having taken a proof with many hundreds of *R. pusillus* in a little cup, the next day I had more than twenty males which were hatched from eggs laid on the bottom during the night. The males were extremely rapid; three times I observed the mating process, the male sitting on the back of the female. Eight days later *R. pusillus* was

only found in very small numbers. Males which were isolated one day in the morning, were always dead before evening; most probably they only live some few hours.

### ***Rattulus cylindricus* (Imhof).**

Tab. III, fig. 8.

**Description.** Body somewhat edged, much broader in front than behind, a soft hyaline cuticula with lines which seem to indicate a rather incomplete lorica; a deep transversal furrow divides the body into a forepart, faintly longitudinally folded in such a way that this part can be folded round the retracted wheel-organ; a posterior part attenuating posteriorly; dorsally this part, when faintly compressed, shows lines which are indicated on the figure. The wheel-organ shows a circle of rather short cilia and on the disc, three tufts of hairs; of these the median is most strongly developed: above it, a very conspicuous fleshy antenna; a broad brain; no eye spot; dorsally a well-developed dorsal antenna and sideways two conspicuous lateral antennæ, each with a strongly developed sensitive hair. Of the excretory organ two short canals, each bearing two vibratile tags, are seen; no contractile vesicle. A very large globular testis, containing the two sorts of spermatozoa, and above it a very large oilglobule, surrounded by an irregular, often quadrangular dark mass. On the sides of the testis two large prostata glands. The testis debouches into a strongly developed, protrusile penis-tube, chitinised, but, as far as I could see, provided inside with cilia and ending in a disc with the penis opening lying centrally. No trace of alimentary canal. The whole body containing numerous oilglobules. Size of male 80  $\mu$ , of female 300  $\mu$ .

*R. cylindricus* is rather common in many of our smaller lakes; in contrast to almost all the other members of its genus it is a real plancton organism; as such it carries its eggs; of the female eggs only one or two; of the male eggs a small chain of three or four eggs; of these females carrying male eggs I have isolated several, hatched the males and seen them in great numbers in my vessels; they were extremely rapid and very difficult to isolate and study. Their form was more flattened than in the other species described; the large oilglobule and the numerous other globules, deposited round the organs, may be regarded as plancton characters.

### **General remarks.**

As the males of *Diurella* have hitherto been entirely unknown, we are unable to indicate the family character of the males. With regard to *Rattulus* it may be pointed out that the males are extremely small, only measuring about  $\frac{1}{3}$  to  $\frac{1}{4}$  of the female. They lack every trace of a foot, the long differently formed toes, and the foot glands so highly developed especially in this family; also, all indications of a carina and thorns on the forepart of the lorica are absent. The body is only a cylindrical or flattened sack with a faintly developed lorica. The wheel-organ is a terminally situated disc, surrounded by a wreath of cilia, and on the disc some bunches of long bristles; when retracted, the forepart of the body is folded over it.

At all events in *R. cylindricus* a well developed antenna; a retrocerebral organ has hitherto not been found, but always a dorsal antenna, and in the male of *R. cylindricus* two lateral ones, symmetrically situated (in the female asymmetrically). An excretory organ may often have been overlooked; it is only found in *R. cylindricus*. The testis is globular, a prostata gland is perhaps always present; peculiar is the long, thin, protrusile, chitinised penis-tube, ending in a disc without a wreath of cilia. No trace of alimentary canal found. The muscle system is slightly developed. Whereas the females are highly asymmetrical, the males are symmetrical animals.

### **Euchlanidæ.**

The family comprises the two genera *Euchlanis* and *Diplois*. The males of *Diplois* are unknown. As far as I know, only COHN has seen and given a more thorough description of a male of an *Euchlanis* (*E. dilatata*). The species of the genus *Euchlanis* are even in the female sex very difficult to distinguish from each other, and a revision most necessary. The main characters are to be found in the size, in the relation between the dorsal and ventral plate, in the anterior and posterior borders of the carapace, in the number of teeth in the unci and in the number of the long hairs on the foot.

At different times I have seen the males of the four species *E. dilatata* Ehrbg. *E. oropha* Gosse (= *parva* Rouss.). *E. triquetra* Ehrbg. and *E. lyra* Huds. As the males are almost all of the same size, and the posterior and anterior borders are subject to great variation and difficult to study upon dead animals, as further the mastax is wanting, and I have never been able to find the long hairs on the foot of the male, it will be understood that it is very difficult to distinguish the males from each other; only the male of *E. triquetra* is always recognisable.

### ***Euchlanis dilatata* Ehrbg.**

Male: Cohn 1858, p. 290.

Weber 1898, p. 580.

Tab. IV, fig. 1, Tab. V, fig. 5.

COHN (1858, p. 290, Tab. XIII, fig. 5—7) gives one of the best descriptions and drawings of a male Rotifer which has hitherto been published.

The male is remarkably large, being 260  $\mu$ , almost as large as the female, the latter being often only 290  $\mu$ . The body is the same as that of the female but the male is much more hyaline. The carapace, the wheel-organ and the foot are formed in full accordance with these organs in the female. On the other hand the whole alimentary canal is lacking. The retrocerebral organ, which is remarkably correctly drawn, is regarded as a brain; no lateral organs; but the dorsal antenna, indicated as "sporn", has been observed. So also are the excretory canals with three or four vibratile tags; it is stated that there exists a contractile vesicle. The testis is described as a long sac with elastic walls. The band which runs from the testis and forwards and which LEYDIG regards as a rudiment of the intestine, is described. A prostata is found. Penis is traversed by a canal, coated with cilia and ends on the first joint of the foot. The sack with light refracting grains over the testis has only been observed in very young animals. Mating process not observed.



WEBER (1898, p. 580) describes the male as follows:

"Le male est morphologiquement identique à la femelle. Il est seulement plus délicat, de taille plus petite et ne possède pas de tractus intestinal. Les organes excréteurs du mâle sont aussi développés que ceux de la femelle et les canaux latéraux se déversent dans une vessie contractile. Le système nerveux, les tentacules et l'organe sacciforme ont la même structure que chez la femelle. La cavité du corps est occupée en grande partie par un long testicule piriforme. Le penis est court, mais de structure normale. Les glandes prostates sont bien développées. La musculature et les organes excréteurs sont faciles à étudier chez le mâle, à cause de la grande transparence du corps et de l'absence de système digestif." Size of female 290–380  $\mu$ , of male 260  $\mu$ .

**Description.** Form of the body the same as that of the female, carapace too almost in full accordance, only a little more hyaline; on the dorsal shield some crests make a peculiar figure which will be better understood when studied in Tab. V, fig. 5; the dorsal antenna is situated where two well marked lines meet each other in the middle lines of the body; laterally, a little from the two posterior corners of the dorsal shield, the two lateral antennæ are found (Tab. V, fig. 5). Ventral plate in the male somewhat larger than in the female; the excavation of the anterior border not so deep as in this sex; foot three-jointed, but when compressed and when the penis is protruded, the segmentation inconspicuous; toes long, well-developed; in my specimens broader than those which are drawn by COHN. I have been unable to find conspicuous foot glands, well-developed in the female sex; also the long tactile hairs seem to be wholly absent. The wheel-organ is highly developed; it consists of a strong ciliary wreath, most probably interrupted dorsally and ventrally; laterally two rather inconspicuous ears; on the disc a median furrow, covered with cilia, terminating in a strong tuft; laterally three pairs of prominences covered with cilia; the two pairs nearest to the furrow; one pair more laterally. The two pairs which are nearest to the median furrow, carry a series of taps, each with a long hair. I have been unable to find the papillæ of the female, mentioned by almost all authors from recent times, and which DE BEAUCHAMP has shown carry the openings of the retrocerebral organ. All in all the wheel-organ of the male resembles that of the female very much. I especially refer the reader to WEBER (Pl. XXI, fig. 21); it is highly interesting, that also in the male we are able to point out the cilia-covered furrow which in the female leads into the mouth, and which may be regarded as closed in the male.

The retrocerebral organ is very large, reaching almost to the middle line of the body; as I have never been able to get a side view of the male, I have not been able to find out if it sends a cul de sac downwards between mastax and brain; the opening outwards I have not been able to see; the organ is filled with numerous areoles which show a polyhedrous structure, caused by pressure. According to DE BEAUCHAMP they derive from the protoplasmatic layer in the bottom of the sac which is due to a vacuolisation of the protoplasma. I refer the reader to the admirable investigations of DE BEAUCHAMP (1909, p. 127). Above the organ is the red eye with a conspicuous lens. On either side of the sac are some large piriform cells

which may most probably be regarded as ganglia cells. Medially through the body is stretched a long, bright band, reaching from the wheel-organ down to the testis, embracing this with two arms. It is a remarkable fact that I have quite distinctly seen, almost in the middle line of the band, on the sides, two pyriform bodies which, according to place and structure, can only be interpreted as gastric glands, only rarely found in the male sex, and not in the other males hitherto known in this genus. I am not quite sure, that the band is not hollow; it seems to contain a number of globules, most probably of oily structure.

Hitherto I have never seen coloured particles, which could be regarded as food in it, but often those bodies which LEYDIG has described as "unverkennbare Reste der Magenzellen, grosse Blasen nämlich, mit Häufchen solcher gelbbrauner Körner welche die Magenzellen aller Rotatorien erfüllen (1857, p. 404)."

The excretory organ with regard to the canals shows great resemblance to that of the female; the number of vibratile tags are three or four; whereas COHN mentions and conspicuously draws a contractile vesicle, I have never been able to observe this; the openings of the canals have not been seen. The large testis, containing a great number of two sorts of spermatozoa, is flanked by two large prostata glands and debouches into a long penis tube ciliated inside and with the opening surrounded by a circle of cilia. Above the testis and shining through the animal is the great globular, hyaline sac-like body, filled with an opaque mass. Size of male 200  $\mu$ , of female 260—380  $\mu$ .

I have met with this male rather often during the time from April to May. The mating process I have not seen, but it was found in different small pools, where *Euchlanis dilatata* was very common, and where I have never seen other *Euchlanis* species than this one.

### ***Euchlanis lyra* Hudson.**

Tab. IV, fig. 2; Tab. V, fig. 4.

**Description.** It is with some doubt, that I have referred this male to this beautiful, but rather rare species; the female is best characterised by the peculiar ventral plate, with its curiously rounded end of the flange, unlike that of any other *Euchlanis*; it is further broadest at the hind end and elliptical in outline; the dorsal plate has no notch behind. In the above-named male the ventral plate had almost straight sides and the posterior edge was slightly excavated, formed in another way than the ventral plate of the female; as the whole form of the male was exactly that of the female, and the male was hatched in the vessel containing the true *E. lyra*, with its characteristic ventral plate, I provisionally refer this male to this species.

There are two auricles, separated from the other part of the ciliary wreath by a short space without cilia; the whole ventrally curved disc was covered with a coating of cilia; dorsally three tubercles coated with long, strong cilia. Fig. 4, Tab. V gives a sketch of the wheel-organ, seen ventrally; as the animal died it was not studied thoroughly enough. The retrocerebral organ was very large, but I could find

no protuberances on the disc into which the organ opened. No gastric glands. Above the large testis was the hyaline sac containing numerous sharply edged, light refracting grains; I got the impression that the two lateral canals opened directly into the sac. This may perhaps be a mistake; it is possible that they turned downwards between the sac and testis and, as might be expected, opened on both sides of the first foot joint, near the opening for the penis; there are three or four vibratile tags upon either side of the lateral canals, but no contractile bladder; with regard to brain, testis, prostata, penis, antennæ, eye, intestinal band and muscle system it is in full accordance with the former species. In the body cavity many oil globules. Size of male 250  $\mu$ , of female 450—500  $\mu$ .

This species was found rather common in some ditches, covered with vegetation, near Hillerød, time May—June; the male was observed on <sup>25</sup>/<sub>3</sub> 1921. I have only seen two specimens, both dying before it was possible to get the wheel-organ fully described; the males appeared in my vessels a week after the samples were taken.

### ***Euchlanis triquetra* Ehrbg.**

Tab. IV, fig. 3.

**Description.** The male has quite the same form as the female; the dorsal plate bears the same extremely high crest as that of the female, and as here is laterally expanded; the lateral furrow between the dorsal and ventral plate is very deep as in the female. When HUDSON (1889, p. 91) says of the carapace in the female that the crest is formed by a "special high thin vertical plate, which rises like a crest from the dorsal surface", I do not understand him. As far as I can see it is the real dorsal plate which is crested in both sexes; in this way it is also drawn in Hudson's figure (Tab. XXIII, 4c). The dorsal occipital edge of the male is not or only slightly notched, whereas this is the case with the hind edge; the foot has a structure differing from that of other *Euchlanis* species; it is without any segmentation, peculiarly hairy, and dorsally bears a protuberance, in which the penis opens; the toes are long, acute, possessing rather conspicuous foot glands. The wheel-organ is formed as a ciliary wreath, most probably with an interruption dorsally as well as ventrally; two rather well-developed auricles; ventrally in the middle line the hairs are very long; ventrally on the disc are some elevations, bearing strong bundles of long setæ. When the animal was dying, and the bristles had almost ceased to strike, I got the impression of two series of peculiar curved, membranelles, inserted medially and ventrally on the disc; similar membranelles have been pointed out by De Beauchamp in the female of *E. dilatata* (1909, Pl. I, fig. 5). As well known the female of *E. triquetra* is extraordinarily hyaline, and this holds good if possible in a still higher degree about the male; seen laterally almost all the viscera are visible through the lateral cleft; the retrocerebral organ is very large, filled with polyhedrous areoles; it sends a short cul de sac downwards to the brain where this bears the large red eye; above the organ is a conspicuous hill, bearing the large dorsal antenna. Now and then I think I have seen the protuberances bearing the openings of the retrocerebral



organ, but they have always been concealed under the bristles of the wheel-organ. There are two lateral antennæ. The intestinal band is rather narrow, running from the brain down to the testis which is embraced by it. There is no doubt that this band is really hollow in this species, containing large globules, most probably of oily structure; it may be shown that the band is widened over the largest globules and narrowed in over the smaller ones; no globules are found in any other part of the body than the band; no coloured food is found. The lateral canals are very conspicuous owing to the hyalinity; they bear six vibratile tags each; there is no contractile vesicle; I have with certainty seen the canals open ventrally on the foot. The testis is long, remarkably narrow, flanked by two long pyriform glands; over them are one or two large, hyaline sacs, in those specimens which I have seen, containing only one single globular opaque mass. The muscles, which are wonderfully conspicuous, run as indicated in the figure. Size of male  $180\mu$ , of female  $450\mu$ . The male has been observed several times in May—June.

#### General remarks.

It will be seen, that the males of the genus *Euchlanis* are highly organised animals, resembling the females in form and structure of the carapace; the wheel-organ is almost in the same stage of development. Characteristic is the remarkably well-developed intestinal band which in *E. dilatata* is provided with gastric glands; in *E. triquetra* it is hollow. There is no contractile vesicle (indicated by COHN for *E. dilatata*). In *E. triquetra* the lateral canals open on the side of the foot. In *E. lyra* I have the impression, that they debouch in the sac, filled with opaque grains; further investigations are here necessary.

#### Salpinadæ.

The family comprises the two genera *Diaschiza* and *Salpina*; three males of *Diaschiza* and two of the genus *Salpina* are known.

##### *Diaschiza gracilis* (Ehrbg.)

Male: Dixon-Nuttall 1903, p. 10.

DIXON-NUTTALL (1903, p. 10, Pl. I, fig. 4a) describes the male

"as a very hyaline, soft, restless male contorting itself into a variety of form, which it is impossible to represent in a drawing. It has a frontal eye, slightly marked clefts, short toes, almost straight, slightly recurved. The sperm-sack fills the greater part of the body-cavity. The three antennæ are to be found in their usual situations. It is without manducatory organs. Length a little more than half that of the female, being  $150\mu$ . Time July."

##### *Diaschiza gibba* (Ehrbg.)

Male: Dixon-Nuttall 1903, p. 7.

DIXON-NUTTALL (1903, p. 7, Pl. I, fig. 1a) describes and figures the male.

"It has the same four plates as the female; the setæ on the foot; the three antennæ; the lateral compression, and the frontal eye; all just like the female. In contrast to those of

the female the toes are decurved, sharp and short. A large sperm-sack fills the greater part of the body-cavity; there are no manducatory organs. It is a remarkably large male  $233\mu$ , the size of the female measuring  $282\mu$ . It is described as very soft and flexible, contracting and elongating itself and in fact contorting itself into all sorts of shapes and sizes. Time April—May."



### ***Diaschiza Hoodii* Gosse.**

Male: Dixon-Nuttall 1903, p. 131.

DIXON-NUTTALL (1903, p. 131, Pl. II, fig. 5i) has described the male as follows:

"It has the four plates, the usual clefts between them and the cervical eye exactly as in the female. The toes are fairly long in proportion to the trunk, thin and decurved. The sperm-sack fills the greater part of the trunk. It is without manducatory organs. Size  $113\mu$ , that of female  $194\mu$ . Time November."

### ***Salpina spinigera* (Ehrbg.)**

Tab. V, fig. 2.

*Diaschiza Hoodii*  
Gosse ♂ after  
Dixon-Nuttall.

Description. Lorica much resembling that of the female. The hind border of the lorica is straight, provided with two strongly curved spines. The wheel-organ, the brain, the eye and the dorsal antenna are in accordance with those of the female; the foot is remarkably well developed, of almost quite the same shape as in this sex. From the testis and to the eye spot, where the mouth is to be found in the female, runs a hollow band in which is a peculiar dark mass, pointed in front. As far as I can see, this is a remnant of the mastax, rudimentary, without any trace of teeth. The testis is very large, globular, provided with a very long ductus seminalis; two prostata glands; the ductus seminalis is coated with long cilia, during the mating process it is most probably turned inside out; the genital opening with a bunch of bristles. Above the testis a globular mass with opaque white, quadrangular grains. No trace of the excretory organ observed; as WEBER has observed it in *S. brevispina* it certainly exists; according to him there are five vibratile tags, but no contractile vesicle. A large oil globule is situated dorsally in the posterior part of the body. As in the female it is very difficult to see any trace of the muscle system and like WEBER I have not ventured to give any sketch of it. There are two small foot glands. Size of male  $150\mu$ , of female  $180\mu$ . It is only with some hesitation that I refer this male to *S. spinigera*. I have only seen a single specimen found 20/V 22 in algæ carpets in Strødam moor near Hillerød. *S. spinigera* was very common in the sample and during the whole season the main form in the little moor.

### ***Salpina mucronata* Ehrbg.**

Male: Weber 1897, p. 98.

— 1898, p. 558.

Tab. V, fig. 1.

WEBER (1897, p. 98, Pl. 4, fig. 3; 1898, p. 558, Pl. 21, fig. 7) has seen a single male.

"Les formes extérieures correspondent à celles de la femelle; seul l'organe rotatoire paraît plus simplifié. La lorica est très épaisse et granuleuse. Je n'ai pu en déchiffrer l'anatomie interne, l'animal étant mort très rapidement. La cavité du corps est occupée en grande partie par les organes genitaux. La testicule est allongé et s'avance jusque sous le cerveau. Le pénis est long, étroit, et sa gaine apparaît unie; il est également terminé par une couronne de cils raides. Vu l'opacité de la carapace, je n'ai rien pu voir des organes excréteurs, ni de la musculature. Pas trace d'organes masticateurs, ni digestifs."

HUDSON (1889 II, p. 83) says that BOUSFIELD has seen the male; but there is no description.

### ***Salpina brevispina* Ehrbg.**

Male: Weber 1897, p. 98.

— 1898, p. 564.

WEBER (1897, p. 98, Pl. 4, fig. 4; 1898, p. 564, Pl. 21, fig. 16) has studied the male.

"Le male est légèrement plus petit que la femelle (200  $\mu$ ). La lorica est bien constituée et ressemble en tous points à celle de la femelle. L'organe rotatoire, le pied et ses glandes ont le même développement que chez la femelle. Les organes des sens sont identiques. Quant au système excréteur, que j'ai réussi à bien voir, vu la transparence de la lorica, il se compose de deux canaux latéraux, portant chacun cinq flammes vibratiles. Les canaux latéraux débouchent de chaque côté du pénis à la base du pied; donc absence de vessie contractile. Les organes digestifs et masticateurs font complètement défaut. Le testicule occupe la plus grande partie de la cavité du corps; à sa base, on trouve les restes du jaune d'œuf. Le pénis est puissant et long; son enveloppe chitineuse est fortement annelée et se termine par une couronne de cils raides et longs. Time: May."

**Description.** Carapace rather thick, almost identic with that of the female, only differing a little with regard to the posterior edge; the posterior spines being a little more acute than in the female. The wheel-organ, the brain, the eye, the dorsal antenna, the foot with the toes and the foot glands are of almost quite the same structure as those of the female. From the testis and to the spot where the mouth is to be found in the female, runs a hollow band; in it is a peculiar dark mass, pointed in front. The whole is interpreted as a rudimentary alimentary canal; the dark mass as a rudiment of the mastax, without any trace of teeth. The testis is very large, globular, provided with a very long ductus seminalis, coated with long cilia; the last part, most probably turned inside out, used as penis; a bunch of bristles at the genital opening. Above the testis some large dark masses, differing in form and size in the different specimens. The excretory canals have been observed, they are provided with four vibratile tags; no contractile vesicle; the canals open near the sexual opening. Round the posterior part of the brain a large number of small reddish globules; no muscles traceable. Size of male 150—180  $\mu$ , of female 200—250  $\mu$ . A few specimens found in algæ carpets 15/V 22 near Hillerød.

### **General remarks.**

It seems as if the males of the family *Salpinadæ* are remarkably large, being two-thirds the length of the female, and apart from the rudimentary alimentary canal



and the want of contractile vesicle as highly organised. This especially holds good with regard to wheel-organ, brain and sensitive organs. The lorica is well developed, corresponding in composition, clefts and thorns with that of female; only it is much softer in the male sex; especially the *Diaschiza* males seem to be very slender animals. The foot and toes are well-developed; the peculiar tuft of hairs characteristic of the genus *Diaschiza* and situated upon the dorsal side of the foot, is also found in the male. The wheel-organ is almost the same as that of the female, but in the centre of the head there are not the projecting lips at the buccal orifice, especially characteristic in *Diaschiza*. In the *Salpina* males a rudimentary alimentary canal with rudiments of mastax without teeth. The two excretory canals are most probably always present with openings near the genital opening. The testis is large, filling the greater part of the body cavity. The genital opening is on the dorsal side of the foot; it is surrounded by cilia.

#### Cathypnadæ.

The family comprises three genera: *Monostyla*, *Cathypna* and *Distyla*. Curiously enough, though some of the species f. i. *Monostyla cornuta* and *Cathypna luna* belong to the most common Rotifers in ponds overgrown with vegetation, males are quite unknown in this family.

#### Coluridæ.

The family comprises the two genera: *Colurus* and *Metopidia*; we only know the males of *Colurus bicuspidatus*, *Metopidia lepadella* and *Metopidia solidus*.

#### Metopidia lepadella Ehrbg.

Male: Gosse 1889<sub>II</sub>, p. 106.

Harring 1917, p. 534.

Tab. V, fig. 3.

GOSSE (in Hudson-Gosse 1889<sub>II</sub>, p. 106) thinks he has seen the male:

"A minute creature, in form a very long cone, tapering to a point, with two slender toes; in front, quite truncate, with a sharp horn projecting from its forehead. No organisation was visible within, save two conspicuous clear vesicles, side by side in the middle of the body, not at all like oil-globules, being irregularly oblong: nor accidental, being found in each of a large number of individuals, seen at different times. A pair of fine lines ran far down the two sides of the body, and in the hinder part was a large web of thin yellowish tissue. Else the whole seemed structureless and of hyaline clearness. It contracted into a shorter oval figure."

HARRING (1917, p. 534, Pl. 91, fig. 1—2)

gives a figure of the male but no description.

Description. Body cone-shaped, without any real lorica, extremely hyaline tapering behind and provided with two well developed toes. A frontal hood, formed as an extremely hyaline plate. Wheel-organ a ventrally placed quadrangular disc, covered with a coating of short hairs, laterally limited by two patches, covered with a similar hair coating; two conspicuous red eyes. The whole body cavity filled with

a greyish mass, containing many small oil globules. In this mass it has only been possible to detect a brain, a large pear-shaped testis with a long ductus seminalis, covered with long cilia. No prostata glands and no protrusile penis observed. Above the testis a hyaline mass, containing many white quadrangular grains. No trace of alimentary canal, excretory organs or antennæ have been detected. There are two foot-glands. Five transversal muscle bands and four longitudinal muscles have been seen. Length of male  $50\mu$ , of female  $150\mu$ .

I have only found one single specimen, found 3/V 22. The females were present in millions in the algæ carpets; many eggs were laid but none which could be regarded as male eggs. Some points in Gosse's description are very unintelligible.

### ***Metopidia solidus* Gosse.**

Male: Wesché 1901, p. 123.

WESCHÉ (1901, p. 123, textfig. 1—4) has observed the female.

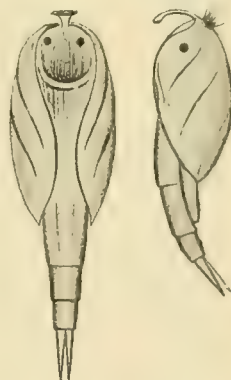
It is mainly described as follows. Carapace not well defined, without the smoothness and symmetry that characterises the lorica of the female; an anterior and posterior edge is observed: form somewhat oblong or rounded. As in the female the foot is divided into four segments. At the end of the second from the base is the ciliated orifice of the penis, while the fourth carries the toes, the joint in the middle of the foot is not so flexible in the female, the toes are pliable and sometimes take a well-defined curve which shows on the lateral view. The "Cowl" or "Pick" on the front is well developed; two eyes are visible, the cilia are long, arranged as in the female. Dorsal antenna is well defined; lateral antennæ approximately in the same place as in the female. Owing to the presence of oil globules, and the denseness of the lorica only little of the internal structure could be seen. No lateral canals of the vascular system are observed; a testis with spermatozoa was found. In one specimen a transparent sac was seen in the dorsal region; this is interpreted as the remains of a digestive system. Time February. Size  $113\mu$ . As the size of the female is 140 to  $170\mu$  the male seems to be remarkably large.

### ***Colurus bicuspidatus* Ehrbg.**

Male: Weber 1898, p. 623.

WEBER (1898, p. 623, Pl. 22, fig. 19—20) is the only one who has seen the male.

"La lorica est semblable à celle de la femelle, mais les bords ventraux des deux plaques de la carapace sont moins convexes, moins repliés sous la face ventrale et laissent entre eux une fente assez large, même dans sa région moyenne. Le bord dorsal des sillons céphalique et pédieux n'est pas échancré. La lorica, moins résistante que celle de la femelle, est marquée de deux plis transversaux obliques et parallèles. Le pied est comparativement plus long et plus vigoureux que celui de la femelle. Il est tri-segmenté et se termine par deux doigts pointus, relativement plus courts que ceux de la femelle. Le pénis fait saillie hors de la lorica, à la face dorsale du pied. Le bouclier céphalique est semblable à celui de la femelle, mais plus étroit. L'organe rotatoire ne comprend qu'une couronne ciliaire. La tête porte deux petits yeux latéro-frontaux. Le tentacule dorsal est bien visible. Time: August."



*Colurus bicuspidatus* ♂  
after Weber.

### General remarks.

The males of this genus seem to be smaller than the females, much more slender and more hyaline. The characteristic chitinous arched plate or hood which surmounts the head in most of the species, is found again in all the males, but a real lorica is but faintly developed. The foot and toes and the two red eyes are in accordance with those of the female. The wheel-organ is mainly a circular or quadrangular, ventrally situated disc, without any special development of the hairs bordering the disc. No sign of an alimentary canal have been found nor of an excretory organ; the testis is large; at the second joint of the foot is the opening for the penis.

### Fam. *Dinocharidæ*.

The family comprises the four genera: *Polychætus*, *Dinocharis*, *Scaridium* and *Stephanops*. WEBER has described the males of the two genera *Dinocharis* and *Scaridium*.

Very often I have seen large maxima of *Dinocharis pocillum*, two times of *Stephanops lamellaris* and several times of *Scaridium longicaudum*. Curiously enough I have never seen the males. In the following are given the descriptions and figures of WEBER.



*Dinocharis pocillum* ♂  
after Weber.

#### *Dinocharis pocillum* (O. F. M.).

Male: Weber 1897, p. 96; 1898, p. 523.

WEBER (1897, p. 96, Pl. 4, fig. 5; 1898, p. 523, Pl. 20, fig. 11) has observed the male.

“Il est beaucoup plus petit que la femelle, il est aussi plus agile. Carapace grise, opaque et mal définie. On n’observe plus la carapace à facettes de la femelle; le corps a une forme plus arrondie. Le grand pied à éperons et long doigts, de la femelle, est considérablement réduit. Ici, le pied est droit, cylindrique, a quatre segments et terminé par deux doigts entre lesquels se trouve une épine courte. La tête est assez développée, protégée par la cuirasse, à couronne ciliaire simple. Cerveau peu visible, portant l’œil; au-dessous de ce dernier se trouve le tentacule dorsal. Je n’ai pas observé de tentacules latéraux. Testicule arrondi; pénis épais, sortant entre le pied et la carapace. Deux globules de jaune d’œuf sont faciles à voir à la base du testicule. On distingue les deux canaux latéraux de l’organe excréteur, mais je n’ai pu découvrir de flammes vibratiles. Seul les muscles du pied sont visible. Time: July.”



*Scaridium longicaudum* ♂  
after Weber.

#### *Scaridium longicaudum* Ehrbg.

Male: Weber 1897, p. 97.

— 1898, p. 529.

WEBER (1897, p. 97, Pl. 4, fig. 1; 1898, p. 529, Pl. 20, fig. 16) has observed two males.

“Le male diffère passablement de la femelle... Le pied est court, cylindrique, à quatre articulations et terminé par deux doigts légèrement recourbés. La lorica est faible et a la forme d’un cône tronqué à sa base, au niveau du pied, et présente une sorte de capuchon recouvrant la tête. Le corps, vu latéralement, a la surface ventrale droite, la surface dorsale



bombée et déprimée vers la tête. L'organe rotatoire est muni de touffes de longs cils sensitifs raides et ressemble à celui de la femelle. On aperçoit, comme chez la femelle, une sorte de capsule transparente sur laquelle repose l'œil. Le testicule occupe une grande partie de la cavité du corps, le pénis est long, mince, terminé par la couronne de cils et entouré d'une forte gaine chitineuse qui s'étend parallèlement au pied et va de la lorica au deuxième anneau du pied; la queue est rayée transversalement. Je n'ai pu voir ni organes digestifs, ni organes excréteurs. Ce mâle est vif et saute à la façon de la femelle. Les muscles du pied sont au nombre de deux paires. Time: July."

### **Ploesomatidæ.**

The family contains one single genus *Ploesoma* with four species: *P. hudsoni* Imh., *P. triacanthum* Berg, *P. lenticulare* Herrick and *P. truncatum* Lev. The males are unknown. With regard to *P. hudsoni* WIERZEJSKI and ZACHARIAS (1893, p. 236) only write that:

Zacharias has observed the male. "Es zeichnet sich durch einen zehenlosen Fuss aus, der wahrscheinlich als Copulationsorgan fungiert. An seiner Ursprungsstelle befand sich eine mit Samen gefüllte Blase."

### ***Ploesoma Hudsoni* Imh.**

Tab. XIV, fig. 5—6.

**Description.** Body with parallel sides; somewhat flattened, a little broader behind, covered with a conspicuous lorica; dorsally provided with a series of thicker, parallel longitudinal lines, two of which forming ellipses open anteriorly; ventrally with a system of transversal ridges in a number of four round a little plate, behind which most probably lies the opening for the penis. No foot observed; in swimming it is always retracted, and I never succeeded in seeing it come out by means of pressure upon the cover. In its anterior part the lorica dorsally bears medially a rather stout tag and laterally some smaller indentations. Wheel-organ a ciliary wreath with rather conspicuous auricles, surrounding a disc, which, when fully expanded, presents some peculiarities; in the middle a cushion-shaped elevation, covered with short cilia and laterally two protuberances, carrying a tuft of long cilia; ventrally on the disc two long, thick fleshy club-shaped antennæ. The whole body quite untransparent, greyish, filled with a peculiar granular mass, in which are imbedded large quantities of oil-globules; of those, one especially is always present; this globule, which is lying dorsally in the posterior part, and medially, is very large; the peculiar foam-structure of the lorica in the female has not been observed in that of the male.

Owing to the intransparency of the body, only very little of the internal structure is seen. No brain is observed; only a dorsal antenna; laterally in two skin folds are seen two strong, single sensitive hairs, long and stiff. Seen ventrally the relatively small testis with the two sorts of spermatozoa has been pointed out, but I have not succeeded in finding the ductus seminalis and a penis; also the whole excretory organ has been undiscoverable. Above the testis is a large globular mass, containing a number of sharp edged opaque grains. No muscle system was observed. Size of male 80  $\mu$ , of female 400—500  $\mu$ . Time 23/VIII 21.

I found the species in enormous masses in a little lake: Klaresø near Hellebæk, North Seeland; there were many pelagic eggs found by ZACHARIAS (1893, p. 35) and APSTEIN (1896, p. 160). Male eggs were not observed. In the samples which besides contained only *Rattulus stylatus*, *Brachionus militaris*, *Polyarthra platyptera*, *Synchaeta pectinata* and *Gastropus styliifer*, the male was rather common; it was unquestionably hatched in my vessels and could not be referred to other species than *Ploesoma*, which was the most common species.

### Gastropodidæ.

In my opinion the fam. *Gastropodidæ* comprises the four species: *G. clavulatus* (Ehrbg), *G. hyptopus* (Ehrbg), *G. minor* Rouss. and *G. styliifer* Imh. Of these species *G. clavulatus* and *G. hyptopus* together with *Notops brachionus* are referred to the genus *Notops* under the fam. *Hydatinidæ*. In the descriptions I find but very little conformity between these two first named species, but as I have never had the good luck to find the large and rare *G. clavulatus* I do not venture to alter their systematical position. If my supposition should be correct the genus *Gastropus* should be divided into two genera one of which should contain *G. clavulatus* and *G. hyptopus*, the other *G. minor* and *G. styliifer*.

The males of this family have hitherto been almost wholly unknown; there exists a very cursory sketch of the male of *G. clavulatus* by Western, and a figure and description of *G. hyptopus* by Wesché, but this differs very much from that which I shall give in the following pages.

#### *Gastropus clavulatus* (Ehrbg.).

= *Notops clavulatus* Ehrbg.

Male: Western. 1892, p. 374.

WESTERN (1892, p. 374, Pl. 25, fig. 6) has given the following description of the male:

The general contour is that of the female even to the deep furrow at the posterior extremity. . . . There is no sign of the foot; the digestive organs are totally absent. No vascular canal, vibratile tags and contractile vesicle are observed. A large sperm-sack. A large ganglion or brain carries an eye spot on its ventral side, and numerous nerve fibres may be traced from it to various parts of the body. The males were hatched from small white eggs. Size  $\frac{1}{40}$ .

#### *Gastropus hyptopus* (Ehrbg.).

= *Notops hyptopus* Ehrbg.

Male: Wesché 1902, p. 327.

Tab. VI, fig. 3—5.

Wesché (1902, p. 327, Pl. 17, fig. 3) gives the following description of the male:

"The male has much the same shape as the female, i. e. a rather globular sack. The head is defined by folds of skin which can be traced on the surface. The body is globose, with a tough skin, which it requires some imagination to describe as lorica. There is the folds of skin on the dorsum. Strictly speaking the foot is absent, but its place is occupied by the penis. The cilia are very long and filiform. The brain is exceedingly large, and comes down

in an elongated mass from the front. At its lower extremity a very large reddish-black granular mass seems to concentrate into a dark-red eye on the ventral side. Four powerful muscles are attached to the brain and cilia. The antennæ are as in the female. There are some minute glands below the orifice of the penis on the ventral side. A curious circular gland, connected with the brain by a long muscle, may have some relation to the contractile vesicle. The penis, which is rather long, is ciliated and kept retracted. On pressure being applied it was protruded through an opening which corresponds with the orifice of the foot in the female. I was able to see the spermatozoa individually in the spermatheca." Size male 127 $\mu$ . Time: Marsh.

**Description.** Body peculiarly shaped, trunk fish-formed, resembling that of the female; as in the female without any conspicuous lorica, but with the same longitudinal keels and furrows along the dorsal edge of the trunk; here the skin seems thicker than in other parts of the body; a very short, truncate foot which can be wholly retracted into the skin. The whole animal very hyaline. The wheel-organ consists of a ciliary wreath, without the two styli characteristic of the female; on the disc which is rather flattened and not protusile as in this sex, stand a number of bunches of long bristles; also the whole alimentary canal is absent. The brain is large with a large red eye; behind this a large, reddish-black mass. Two nerves to the dorsal antenna and two lateral antennæ. Lateral canals with three or four vibratile tags; no contractile vesicle. Testis very large, almost globular with a peculiar form; two prostata glands and above them two peculiar irregularly formed cells, connected with the testis and moving together with it and almost incessantly. A peculiarly shaped foot hardly ever seen during swimming; it is undivided and has no toes; dorsally is the opening for the penis which, when fully stretched out, is much larger than the foot, this being placed laterally, only as a small appendix. The testis opens into a ductus seminalis which is coated with cilia and ends in a bunch of cilia. Above the testis many oil globules. There are five transversal muscles, running from the dorsal keels downwards; four pairs of longitudinal muscles for the wheel-organ and two short muscles for the foot. The males resemble young, newly born females very much. Size of male 80  $\mu$ , of female 360  $\mu$ . Time 1/V 21.

As will be seen, there is not the best harmony between WESCHÉ's description and mine; WESCHÉ has observed the place of the antenna; what he regards as a gland connected with the brain and what he supposes to have some relation to the contractile vesicle, I do not know; his description of the penis differs very much from what I have seen.

### **Gastropus stylifer Imh.**

Tab. XIV, fig. 2—3.

**Description.** Body elliptical, attenuated behind with a rather thick lorica; hyaline, no strongly marked colours. A dorsal plate carrying medially and anteriorly a shield-like structure with parallel sides and an acute point. The wheel-organ which is wholly retractile, consists in a ciliary wreath, contouring a disc which carries some bunches of cilia and as far as I have been able to see one single digitiform thick fleshy antenna. A large brain upon which I have been unable to



see any eyespot, but over the forepart of the brain two bright double, contoured light refracting spots, which are most probably openings from a retrocerebral organ which has not been observed. Neither dorsal nor lateral antennæ observed; nor excretory organs; alimentary canal seems to be wholly wanting. A large piriform testis, containing two sorts of spermatozoa, ending in a ductus seminalis coated with cilia and with a tuft of small cilia at the opening, this situated somewhat ventrally; large prostata glands. When swimming the animal shows no peculiar structural features behind, but when it is pressed below the cover a little tap appears, provided at its tip with a styliform body, perhaps a seta. In this tap lies a rather large gland-like body, immediately over which the prostata gland lies. I regard this tap as the rudiment of a foot, and the gland as the foot gland. Above the testis lies a very large light refracting oil globule and between it and the brain a large globular opaque body, containing numerous sharply edged small bodies. Only a few longitudinal muscles have been seen. At a first glance and, when the animal is swimming, the whole body is almost quite opaque, filled as it is by a greyish mass with many small oil globules. It is only by means of pressure that the internal structure has been somewhat elucidated. Size of male 80  $\mu$ , of female 170—200  $\mu$ . Time 1, VIII 21. In a plancton sample which only contained this species, *Polyarthra* and *Synchaeta*, 10 specimens of the above described peculiar male appeared.

#### Ascomorphidæ.

This little family comprising the two genera *Ascomorpha* and *Anapus* may best be connected with the fam. *Gastropodidæ*; DE BEAUCHAMP refers the genus *Ascomorpha* to this family. It differs from it in very essential points; its systematic position and restriction has always been difficult; owing to want of foot it was formerly referred to the fam. *Asplanchnadæ*, with which it has no affinities at all. It comprises such different forms as *Ascomorpha* (= *Sacculus*) *viridis* Gosse; *Ascomorpha saltans* Bartsch (= *A. agilis* Zach). Also the genus *Anapus* is referred to this group.

In my opinion the whole group is very unnatural. The *Ascomorpha* (= *Sacculus*) *viridis* Gosse has only slight affinities to the other *Ascomorpha*-species. *A. saltans* Bartsch, which is perhaps identic with *A. agilis* Zacharias is well known to many planctologists, but almost unknown in the literature relating to Rotifera; the genus *Anapus* differs in all essential points from *Ascomorpha*.

*Sacculus viridis* is common in the vegetation zone of smaller ponds; it carries its eggs, female as well as male eggs.

*Ascomorpha saltans* and the genus *Anapus* with the two species *A. testudo* Lauterb. and *A. ovalis* Bergend. are all typical plancton organisms in the pelagic region of smaller lakes, but especially in the central free parts of ponds. The species prey upon the Dinoflagellata (*Ceratium hirundinella*, *Peridinium*), which they suck out, whereupon the empty hyaline carapaces fall to the bottom. Their maxima coincide with those of the *Dinoflagellata*. The eggs are laid upon other plancton organisms, especially *Uroglana volvox*. In my opinion the genus *Anapus* may be

referred to a special family. As far as I can see an anus is wanting, as well in the *Ascomorphidae* as in *Anapodidae*; characteristic of both is a thick fleshy antenna, situated on the disc of the wheel-organ.

I hope I shall later on be able to return to these very interesting and but slightly studied animals. The males are almost quite unknown. Of *A.* (= *Sacculus*) *viridis* GOSSE (1856, p. 320, Pl. XV, fig. 26) has given a small but rather good drawing of the male: He only says: "I could not detect any eye, nor any internal organization; nothing but a confused assemblage of granules and globules; even the ordinary opaque masses were not present. The form somewhat resembled that of an amphora with a short wide neck; the frontal cilia were very large, but the motion was not rapid, nor was the animal wild as male Rotifera usually are. Female  $\frac{1}{150}$  in., male  $\frac{1}{270}$  in.

I have often had females with male eggs and hatched the males; these commonly appear in spring; the males are extremely small; I have always failed in getting a good drawing of them. Tab. XIV, fig. 4 gives a little sketch of the animal.

### Pterodinidæ.

The family comprises the two genera: *Pterodina* and *Pompholyx*; the males of the genus *Pompholyx* have hitherto been unknown; of the genus *Pterodina* only ROUSSELET and MARKS & WESCHÉ have described the males.

#### *Pterodina elliptica* Ehrbg.

Male: Rousselet 1898, p. 27.

ROUSSELET (1898, p. 27, Pl. IV, fig. 4 e, f.) writes.

"In outline it is very narrow, elongated, and quite unlike the female. It has a decided, but rather soft, lorica and two red eyes in front, but is devoid of jaws. The copulatory organ projects dorsally above the foot, which is of usual structure and ciliated at the end. Size of male 127  $\mu$ , of female 136  $\mu$ ."

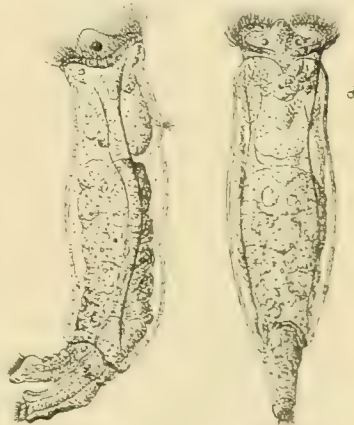
WEBER (1898, p. 653) only states that the male has been observed by several naturalists.

#### *Pterodina patina* Ehrbg.

Male: Marks & Wesché 1903, p. 509.

The Male has been observed by MARKS & WESCHÉ (1903 p. 509, Pl. 26, fig. 3).

"Seen laterally, rather vermiform, resembling a young *Proales petromyzon*. Dorsally, somewhat broad, but having no approximation to the plate shape of the female. Head, rather short, without quasi-auricles as in female; constriction of neck not well marked. Body, rather broad, but fairly long; edge of carapace visible laterally, and two folds on the posterior sides, when viewed dorsally. The two muscles, so prominent in the female, and used to retract the head, are present and well marked, and best seen on the dorsal view. Foot, short, stout, retractile, with a gland at the extremity. Toes, none. Cilia, moderately long. Brain, large, occupying all the head and sending



*Pterodina elliptica* ♂  
after Rousselet.

a long process to the dorsal antennæ. Eyes, two, red and well marked. Antennæ, all three in the centre of the body, almost in a line. Setae very fine and difficult to make out. Digestive system, represented by a hyaline membrane, appearing to be in an atrophied condition. Vascular system, faint; no contractile vesicle seen. Generative system, very large; spermatozoa masses in testis; orifice of penis slightly ciliated and situated down the dorsal side of the foot; no granular masses as in *Brachionus*. Size male 127–135  $\mu$ . Time May 12th."

ROUSSELET (1908, p. 27) says that,

according to a letter to him, BILFINGER has observed the male, which agrees with that of *P. elliptica* in every particular.

It seems that also DIEFFENBACH (1912, p. 196)

has seen it and confirms the above named observation.

Though I have seen very large maxima of *P. patina* especially in the winter season I have failed to get the male.

### **Pompholyx sulcata** Hudson.

Tab. XIV, fig. 1.

**Description.** Body globular, without the four longitudinal furrows, characteristic of the female; the skin very soft, no regular lorica; a dorsal surface slightly separated from the ventral one by means of a rather indistinct line, ending round the opening for the testis. Near the forepart of the body a transversal line; before it the chitine folded longitudinally, so that the body, seen from the front, when the wheel-organ is drawn in, is crater-shaped. The wheel-organ consists only of a single row of rather short cilia; as far as I have been able to see, the disc is not bare as in the female, but covered with cilia. The band of cilia encircles the disc without any interruption ventrally in the middle line.

Below the ciliary wreath a series of indistinct hypodermal cells; a large brain, carrying two red eyespots, each with a lens, situated in a spot, corresponding to that of the female. I have not been able to see either dorsal or lateral antennæ; as far as I know, they have never been observed in the female either. There is not the slightest trace of an alimentary canal; nor have I seen any part of the excretory organ. There are two pairs of rather conspicuous muscles, running from the forepart of the wheel-organ, one pair fastened near the middle of the body, the other nearer to the hindpart. The whole animal seems to consist almost entirely of an extremely large pyriform testis, filling more than two thirds of the body cavity. Scattered over and round the testis are large oil globules, different in number and size; the testis itself contains rather few spermatozoa; I have hitherto not seen any of the staff-formed ones. No prostata glands are found, and I have seen no penis. When strongly contracted the body tapers behind, into two small tubercles, limiting the opening for the testis; this opening is rather large and encircled by a row of short cilia. Size of male 40  $\mu$ , of female 90  $\mu$ . Time 25/VIII 21. I have never seen the copula, but very often observed the male rotating round the female. The males were hatched in great numbers from the male eggs, carried by the females in my vessel.



### Pedalionidæ.

The family comprises the three genera *Triarthra*, *Tetramastix* and *Pedalion*. The males of the peculiar genus *Tetramastix* first described by ZACHARIAS 1898 (p. 132) and later by ROUSSELET (1906, p. 431) are unknown.

PLATE has described the male of *T. breviseta*, but the description is very short and no figure is given. WESCHÉ has figured and described a male, which he refers to *T. longiseta*, but whatever WESCHÉ has found, it is very difficult to understand that it is a male of the genus *Triarthra* he has observed.

#### *Triarthra longiseta* Ehrbg.

Tab. XV, fig. 1.

ROUSSELET (1903, p. 176)

has observed the male but there exists no description).

WESCHÉ (1902, p. 325, Pl. 17, fig. 1 a, b) has perhaps seen the male.

"The head is well defined, and its limits are marked by several folds of skin. The body is broad and stout. The foot is well separated from the body, without toes, but with two short setæ on the orifice of the penis, which goes down to the extremity of the foot. . . There is a large brain with a conspicuous sub-circular eyespot. Four powerful muscles are attached to the brain and cilia. . . The dorsal antenna is connected with the brain by a flexible tube. The lateral antennæ are well marked, and have the usual tapering gland, noticeable in the female. There is no trace whatever of a digestive system. The lateral canals are well marked, and the contractile vesicle large. The skin is thick, but flexible. A large spermatheca tapers down to the end of the foot, which practically forms the penis. Size 70—90  $\mu$ . Time: February."

**Description.** Body elongate, attenuated behind, soft, hyaline, two or three times slightly constricted. The wheel-organ a closed ciliary wreath without any tongue-like projection ventrally. In the middle of the disc a peculiar broad rectangular projection of a proboscis-like appearance; it is covered with a coating of very short hairs and, near its base, bears the two semiglobular red eyes, each with a lens. There is a brain, but no retrocerebral organ; neither dorsal nor lateral antennæ have been observed. Only a large pyriform testis is found, containing two sorts of spermatozoa and ending in a long "penis" tube ciliated in its interior. During the pairing-process the body behind is acuminate; in this and in the following species the penis is really only the acuminate hindpart of the body. Near its opening this latter bears two small chitin-pieces, which can be folded in and out; there is no ciliary wreath round the opening, but a little above it two strong sensitive hairs. Round the testis two prostata glands. A faintly developed system of longitudinal muscles has been observed, but no conspicuous transversal muscles. The body is extremely flexible, when not compressed much, more globular than the drawing shows, but during the mating process still more attenuated behind. The body contains very many oilglobules often arranged in a half circle round the testis. Size male 80  $\mu$ , female about 170. Time 15/V 21.

As mentioned above WESCHÉ has described and figured the male; according to the figure, with regard to the opening for the penis, it may be regarded as pos-

sible, that he really has observed the male, but besides it must be emphasised that some main points in the structure have been overlooked or incorrectly interpreted. This especially holds good with regard to the proboscis-like projection, within the ciliary wreath. WESCHÉ further indicates one single eye. It is highly remarkable, that he has further found dorsal and lateral antennæ, excretory canals and even a large contractile vesicle and a foot well separated from the body; neither PLATE nor myself have in any of the males belonging to this genus been able to see anything of this kind. The contractile vesicle indicated by WESCHÉ in his text is not found in his figures.

In the sexual periods the males occur in great numbers and may then be caught in the lighted borders of the vessel.

### **Triarthra mystacina** Ehrbg.

Tab. XV, fig. 2.

**Description.** The male resembles that of *T. longiseta* very much. The proboscis-like projection is much shorter; I have been unable to find any organs but the very large testis and the two red eyes; no prostata glands: the penis is shaped as in *T. longiseta* but no sensitive hairs have been found. Size of male 70  $\mu$ , of female 200  $\mu$ . *T. mystacina* is extremely common in smaller ponds. During the two maxima April—May and Sept.—Oct. the males occur in great numbers.

### **Triarthra breviseta** Gosse.

= *T. cornuta* Weisse.

Male: Plate 1886, p. 21.

Tab. XV, fig. 3.

PLATE describes the male as follows.

“Die Männchen haben ungefähr eine Grösse von 0,08 und in der Gestalt viel Ähnlichkeit mit den Männchen der noch zu beschreibenden *Hertwigia volvocicola*. Sie sind cylindrisch, besitzen vorn einen Cilienkranz, über den die Cuticula, ohne weiter bewimpert zu sein, halbkugelig vorspringt. In den daselbst gelegenen Matrixverdickungen, vielleicht auch in Verbindung mit dem grossen Gehirn, sitzen zwei rote Augenflecke, die wie bei den Weibchen deutliche lichtbrechende Körperchen erkennen lassen. Nach hinten verjüngt sich das Tier, und da der enge, flimmernde Ausführgang des Hodens am aboralen Körperende ausmündet, dient dieses zugleich als Penis. Gehirn und rudimentärer Darm bieten nichts Bemerkenswerthes. Tastbüchel, Wassergefässe und contractile Blase habe ich bei der steten Beweglichkeit des Tierchens vergebens gesucht.”

**Description.** The male resembles those of the just described two species very much, but the proboscis-like projection is very short, often rising only a little above the ciliary wreath. Of inner organs I have only been able to observe the brain and the very large testis. The penis is very short; the peculiar chitin staffs in the two other species I have not found here. Size of male 60  $\mu$ , of female 120  $\mu$ .

As mentioned above PLATE has seen the male, but gives no figure; his description and mine agree fairly well.

The species is rather rare. On 17/V 21 I had the good luck to get a sample from a little outdrying pond near Hillerød, containing a maximum of this charming little creature, some of the specimens carried male eggs, and from them the male was hatched.

### Pedalion.

The old order *Scirtopoda* originally contained only the genus *Pedalion* with the two species *P. mirum* Huds. and *P. Fennicum* Lev. In 1899 (p. 142) I referred *Triarthra* to the fam. *Pedalionidae* and DE BEAUCHAMP (1909, p. 41) has adopted this view. One of the most striking structures in *Pedalion* are the two stylate ciliated appendages on the posterior dorsal surface, unique in Rotifera. As they are totally absent in *Triarthra* it should really be regarded as rather hazardous to refer *Triarthra* to this family, but as these appendages are also totally absent in one of the two known species of *Pedalion* *P. Fennicum* Lev. they seem to have no particular systematic value.

### *Pedalion mirum* Hudson.

Male: Hudson-Gosse 1889II, p. 133.

Tab. XIV, fig. 7—8.

HUDSON GOSSE (1889II, p. 133, Pl. XXX, fig. 1 h, 1 g).

The male is the merest caricature of the adult female. The large shapely corona, with its flowing curves has become a ciliated knob; the six limbs, with their fan-shaped plumes, have been altered into three little stumps, with a bristle or two at the end of each; even the huge ventral limb has vanished, and the whole creature has shrunk up to barely one-fifth of the length of the adult female. It swims very differently from its mother; for it spins constantly round its own length, like a joint on a spit, while at the same time moving forward. Now and then it jerks its side limbs, and it uses them to free itself from its shell. There are two longitudinal muscles for retracting the head and a pair of red eyes, but I could discover no other internal organs except the testis and penis. This latter I have seen protruded to a length quite equal to that of half the animal. Size: female  $\frac{1}{125}$  inch, male  $\frac{1}{575}$ .

**Description:** The male is remarkably broad, almost globular with the forepart rather sharply removed from the other part of the body; directly backwards protrudes dorsally a thick humpback-like protuberance; laterally two others are found; these protuberances differ in form in the different specimens and most probably in the same specimen; they may be rather broad, faintly acute, very broad at base with a sharply defined wing-like outer part; they end in a bunch of about five very short bristles. Seen from above, the body is rounded behind. The wheel-organ consists only of a ciliated disc, the marginal cilia of which are somewhat longer than those in the middle of the disc. Of internal organs I have only been able to observe a large brain with two curved red pigment spots, each with a lens and a very large globular testis, containing comparatively few spermatozoa of both sorts. There are no prostata glands. The penis is remarkably long, almost half the length of the body, traversed by a long canal, covered with cilia; at the apex a wreath of short cilia. If the penis in this genus too, is really only the posterior part of the body, drawn out when it is to be used as a pairing organ, or if it is a real organ, concealed in



the body, I do not know; when the animal swims, it seems as if it is wholly withdrawn into the body. At all events the ductus seminalis may be able to be elongated and again abbreviated in a very high degree. Size of male 50  $\mu$ , of female 350—400  $\mu$ . Time 25/VIII 21.

As mentioned above, only HUDSON has seen the male; our descriptions and drawings agree rather well; I have however never seen such long setæ as HUDSON describes and figures; also the penis is much thicker. It will be understood, that the male is extremely reduced; of the six "limbs" only three are present and these only transformed into very short, fleshy protuberances with a few stiff bristles. The two ciliated straight processes behind on the body of the female are totally absent in the male.

In the sexual period in August the males are extremely common.

#### General remarks.

Common to all the males belonging to this family is the extreme reduction; the wheel-organ consists of a wreath of cilia, encircling a disc covered with cilia, in *Triarthra* provided with a proboscis-like organ, but dorsal and lateral antennæ have not been observed. There are two eyes, a brain. Of inner organs only the testis has been observed. Perhaps in all species the hindpart of the body is acuminate during the pairing process and then used as a penis.

#### Melicertidæ.

Of the Melicertidæ genera the males are quite unknown in the genera *Oecistes*, *Limnias* and *Cephalosiphon*; also the males of most of the other species are very badly described; well known is only the male of *Lacinularia socialis*, described by HAMBURGER.

#### *Conochilus volvox* Ehrbg.

Male: Cohn 1862, p. 205.

Hlava 1908, p. 28.

Tab. XV, fig. 4—5.

COHN (1862, p. 205, Tab. 21, fig. 16—19).

Die Gestalt lässt sich mit einem langen Sack vergleichen der vorn abgestumpft ist, nach hinten kreiselförmig sich etwas verjüngt. Das vordere Kopende trägt den flimmernden Wimperrand, der jedoch weniger ausgearbeitet ist, wie bei den Weibchen;.. der Stiel und Fuss läuft in einem Wimperbuschelaus. Verdauungsapparat fehlt ganz; das Wassergefäßsystem wurde nicht deutlich, ist aber wohl vorhanden; Gehirn gross, eiförmig; zwei rothe Augen mit brechender Linse und Pigmentumhüllen. Ein grosser birnförmiger Hoden mit den Spermatozoiden vollgestopft. Der Hoden führt in einen Samenleiter, der nach aussen in einen besondern Penis mündet; Höhle und hinteren Rand desselben flimmern.

HLAVA (1908, p. 28, fig. 9 D).

"Das Männchen ist klein walzenförmig. Die Krone ist einfach, in der Mitte des Räderorgans erhebt sich ein stumpfer, zwei hellrote Augen tragender Kegel; die Augen sind mit

deutlichen Linsen versehen. Verdauungsapparat fehlt; anstatt desselben ist ein umfangreicher Hoden entwickelt. Penis ist kurz und liegt auf der Dorsalseite nahe bei dem Körperende; dieses ist verengt und bewimpert". Size of male 50  $\mu$ , of female 500  $\mu$ .

**Description.** Male conical about four times broader in front than behind; wheel-organ an apically placed disc, encircled by a row of cilia. In the middle of the disc a cone-shaped projection, covered with short cilia and provided with two red eyes with well-developed lenses. The interior of the body a greyish mass which only allows of a very superficial study. The brain is undoubtedly present but its contours only faintly observable. Not the slightest remains of an alimentary canal or excretory organs have been observed. There is a large pyriform testis and a ductus seminalis, covered with cilia in its interior; there are two well developed foot glands. The genital opening apically; it is surrounded by cilia; the last part of the ductus seminalis may be turned inside out and during the mating process the body acuminate. I have not been able to see the slightest sign of transversal muscles, but according to the movements of the animal, they are undoubtedly present. Of longitudinal muscles only two slanting muscles have been observed. In the greyish homogeneous mass are imbedded a lot of smaller and larger oil globules; most conspicuous are a few very large ones, commonly situated dorsally before or above the testis. Size of male 50  $\mu$ , of female 600—650  $\mu$ .

On 27/IV 22 colonies of *C. volvox* were found in which resting eggs as well as very minute eggs were found. The next day extremely minute creatures were found encircling the coronas of the females. They were isolated and ascertained to be males. They were incredibly variable in form. Encircling the coronas of the females, they bent the body in all directions simultaneously; it looked as if they were dancing a regular cakewalk round the selected individuals of the colonies; often more than twenty males simultaneously encircled a single colony; then it very often happened that two males butted against each other and then were flung out of their orbits, away into the "empty" space, where they whirled round restlessly till they again touched a colony in one of their large circles. I have tried in fig. 5 (Tab. XV) to give a sketch of such a spasmodic male; it will be seen that the ductus seminalis has been turned inside out and the cilia, now covers a distended ballshaped mass, upon the tip of which the genital opening is seen. For a moment the males were often fastened to the corona or directly below it; most probably this was the pairing act, but it did not last more than a fraction of a second.

### ***Conochilus unicornis* Rouss.**

Male: Rousselet 1892, p. 276.

Hlava 1908, p. 28.

ROUSSELET (1892, p. 276, fig. 6) writes.

"The male is a small pear shaped creature, with a small ciliated head and a large wreath of cilia just below on a wider shoulder. Two red eyes in the head are conspicuous; the body cavity is wholly taken up with the spermsack, and the pointed lower end is ciliated as usual."

HLAVA (1908, p. 28, fig. 10 c) writes:

"Das Männchen ist klein, birnförmig; der Kopf ist klein, bewimpert und ragt auf dem verbreiteten vorderen Körperende empor; die Krone ist einfach und mit langen Wimpern versehen. Zwei rothe Augen deutlich. Der Hoden ist mächtig und nimmt die ganze Leibeshöhle ein; das verengte Hinterende ist bewimpert."

**Conochiloides natans (Seligo).**

Male: Hlava 1908, p. 34.

HLAVA (1908, p. 34) writes:

Das Männchen ist kegelförmig, farblos; das Vorderende des Körpers ist kegelförmig erhöht und auf dieser Erhöhung befinden sich zwei rote, mit deutlicher Linse versehene Augen. Die Krone ist einfach. Die Spermatozoen sind ungemein gross, und der Hoden nimmt den grösseren Teil der Leibeshöhle ein. Das hintere Ende des Körpers ist bewimpert. Size male 80—100  $\mu$ , female 300—500  $\mu$ .



*Megalotrocha  
alboflavicans*  
Ehrbg. ♂ after  
Hlava.

**Megalotrocha alboflavicans Ehrbg.**

Male: Anderson 1889, p. 348.

Hlava 1908, p. 38.

ANDERSON (1889, p. 348, Pl. 20, fig. 3) writes:

"The males were moving in and out of clusters of the female, but I did not see actual connection. There is a certain amount of resemblance to the male of *Lacinularia*, the chief difference being the presence of a very large, clear, circular space, situated in front of the sperm sack which had all the appearance of a contractile vesicle, though I did not see any contraction. The body is cylindrical with a foot projecting from the lower side. The foot glands are very large; the large nervous ganglion has branches to the antenna and to the two eyes, and one proceeding backwards embracing the top of the contractile vesicle. The integument, which is very transparent, occasionally takes the ringed appearance noted above as occurring in the female. There is a regular network of muscles. The cilia surrounding the head are large, setting up a strong current."

HLAVA (1908, p. 38) writes:

Das Männchen hat einen walzenförmigen, hinten in einen kurzen konischen Fuss verengten Körper. Der Räderapparat besteht aus einem einfachen Kranze von starken, rege schwingenden Wimpern. Der Hoden ist gross, vor ihm befindet sich ein grosser, heller, kreisförmiger Zwischenraum, ein Rest der Verdauungsapparates. Das Hirnganglion ist gross, zwei Augen und Dorsaltentakel deutlich. Die Fussdrüsen sind gross. Das Integument ist sehr durchsichtig. Penis ist kurz, bewimpert, zurückziehbar. Size Male: 160  $\mu$ , Female 1000—2000  $\mu$ .

**Megalotrocha procera Thorpe.**

Male: Thorpe 1893 a, p. 151.

THORPE (1893 a, p. 151) writes:

I had the good fortune to find the male, the anatomy of which follows the usual type, possessing a circular wreath of cilia, two bright eyes, a foot and sperm-sack with penis.



**Megalotrocha semibullata** Huds.

Male: Thorpe 1889, p. 614.

THORPE (1889, p. 614, Pl. XII)

gives a short description and a very insufficient figure of the male.

**Lacinularia socialis** (Pall).

Male: Hudson 1875, p. 75.

Plate 1886 a, p. 4.

Hudson Gosse 1889, p. 86.

Hlava 1908, p. 46.

Hamburger 1907, p. 625.

Wierzejki 1893 a, p. 47.

PLATE (1886 a, p. 4) describes the male but gives no figure. In the description the following points are of special interest.

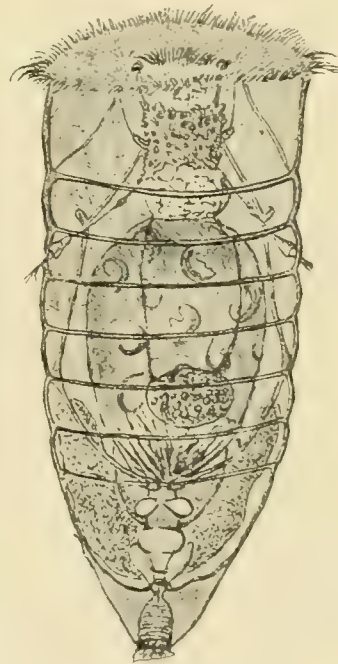
The males are only  $\frac{1}{5}$  the length of the female; body cylindrical with a bunch of cilia near apex. Wheel-organ a wreath of cilia round a vaulted disc with a bunch of cilia at its top. Brain large, quadrangular. A dorsal organ but no lateral organs and two red eye-spots observed. A rudimentary alimentary canal used as suspensor testis. Two lateral canals with vibratile tags, no contractile vesicle. A very large piriform testis; vas deferens coated with cilia; a penis. Prostata gland. Two sorts of spermatozoa.

HUDSON-GOSSE (1889, p. 86, Pl. 8, fig. 1 c) writes:

The male has a conical head fringed with a wreath of long cilia, a cylindrical soft trunk, and a short, pointed, ciliated foot. There are strong longitudinal muscles for withdrawing the corona into the trunk, and several transverse muscle bands in the integument. The nutritive system is wholly absent. Two secreting foot glands are present, as well as the lateral canals and their vibratile tags. Several times I thought I caught sight of the edge of the contractile vesicle, behind the upperpart of the sperm sack. There is a large nervous ganglion, sending threads to a dorsal antenna and two red eyes. A large sperm-sack fills nearly the whole trunk, and ends in a broad, tubular ciliated and protrusile penis.

HLAVA (1908, p. 46, fig. 14 c).

Die Männchen haben einen walzenförmigen Körper, welcher mit einem stumpfen Fuss versehen ist. Vor dem Ende dieses befindet sich auf der Ventralseite ein bewimpertes Grübchen. Der Hoden ist birnförmig, gross und nimmt in der Regel die ganze Leibeshöhle ein. Die Excretionsorgane münden am Anfang von Vas deferens ein. Penis ist röhrenförmig, bewimpert, zurückziehbar und ist mit einem halbkreisförmigen Hornring versehen. Beiderseits sind drüsige Zellen gelegen, welche wahrscheinlich die Funktion der Prostata haben. Oberhalb des Hodens sieht man den Rest des Verdauungskanaals als einen Streifen von veränderlicher Breite und häufig mit zahlreichen Vakuolen. Das Gehirn hat die Form eines Rechteckes. Zwei Ventraltentakel und eine dorsale sind gut sichtbar. Die Augen sind mit deutlicher Linse versehen. Die Männchen schwimmen



*Lacinularia socialis* ♂ after  
Hamburger.

frei in der Nähe der Kolonien und zwar 3—7 bei einer Kolonie; nur bisweilen befestigen sie sich. Size Male: 300—700  $\mu$ . Female 1500—2000.

HAMBURGER (1907, p. 625, Tab. XXXI) has given a very thorough description of the male. The following is a condensed abstract of her text.

The body of the male is somewhat conical; the coronal disc somewhat vaulted; encircled by a closed ciliary wreath and carrying on its top a bunch of cilia and other cilia spread over the disc. The hypodermal cells large and regularly arranged. Brain rectangular, giving off nerves for the two red eyes and for the two lateral organs lying between the second and third transversal muscle, and for the dorsal organ, which has not been observed with certainty. It is of interest that HAMBURGER has pointed out an oesophageal commissure only rarely observed in the Rotifera: *Discopus* Zelinka (1888, p. 235) and *Conochiloides* (HLAVA 1905, p. 282). No alimentary canal, but rudiments between testis and the hypodermal cells of the wheel-organ; even a rudimentary mastax is supposed. Two lateral canals which are supposed to be in connection with each other by means of a transversal commissure beneath the brain; they debouch in the proximal part of vas deferens. The number of vibratile tags is not indicated, but "Treibwimpern" in the lateral canals are observed. The testis is very large and contains two sorts of spermatozoa; the vas deferens (= ductus seminalis) is built of a layer of ring muscles and covered inside with a coating of long cilia. Two prostata glands; to the posterior part of vas deferens two muscles are attached, which, according to HAMBURGER, come into action when the spermatozoa are to be forced out. After a restriction the vas deferens is again expanded and coated with long cilia; there is no penis, but HAMBURGER correctly supposes that it is this part of vas deferens which, when turned inside out, acts as a penis. The opening of vas deferens is situated dorsally. Over the testis an opaque mass, which Hamburger in accordance with PLATE regards as a remnant of a rectum. Below the genital aperture on the very apex of the body a cilia-coated sucker is found, into the bottom of which two glands open. These glands may be homologous with the foot glands of the female; the vasa deferentia for these glands are swollen and used as reservoirs for the secretions of the glands. Seven or eight transversal musclebands are indicated, further the great retractors of the wheel-organ. Length of animal 200—300  $\mu$ . HAMBURGER has given a valuable contribution to the spermatogenesis and pointed out the great difference between the two sorts of spermatozoa. PLATE and HAMBURGER suppose that the males fasten themselves by means of their sucker upon any part of the body and that the stafformed spermatozoa are used as weapons by means of which the bodywall is pierced. The mating process has not been observed.

The species was found in Gudenaå twenty years ago. It occurred here in countless numbers, and in July the males swarmed round the colonies. As the animal was observed on a journey, it was only badly drawn; later on it was found on the underside of the leaves of *Nymphaea* in a pond near Hillerød (Carlsø); in 1920 when the colonies should have been collected a boat could not be obtained. Finally in 1921 it was found in Susaa near my summer laboratory, and I had good opportunity to study the male. Comparing my description with that of Hamburger I could find no differences and I therefore refer the reader to hers.

#### **Oecistes mucicola Kell.**

Male. Western 1891, p. 321.

WESTERN (1891, p. 321, Pl. XXI 1 c) writes:

"I also found what appears to be the male, though I did not actually see it hatched from the egg."

***Limnias ceratophylli* Schrank.**

Hudson-Gosse 1889, p. 76.

GOSSE in HUDSON-GOSSE (1889, p. 76, Pl. VI, fig. 7) states

that he has seen a young animal push out of the tube; he regards it as a male; but it has a mastax; testis is not seen. It is only from its manners that Gosse supposes that it might be a male.

***Melicerta ringens* Schrank.**

Male: Bedwell 1878, p. 249.

Joliet 1883, p. 165.

Hudson Gosse, 1889, p. 71.

Weber 1898, p. 288.

Hlava 1908, p. 71.

BEDWELL (1878, p. 249) according to HUDSON & GOSSE (1889, p. 71) supposes that he has seen the male and gives a description of its behaviour.

As he however maintains that he has observed trophi and a forked foot, it is more probable, as HUDSON states, that he has seen another Rotifer f. i. one of the *Notommatidae*. When the tubes were broken up in Dchr. BEDWELL found the presumed males in them; in one single tube four individuals. It is also conceivable, that we here have to do with young females.

JOLIET (1883, p. 165) gives a rather exhaustive description but rather rough figures (pl. XIII, fig. 51; pl. XI, fig. 11). The following is a summary of the description.

The male resembles the larva of the female; the coronal disc is covered with cilia; there are two red eyes with lenses; the body cylindrical with a conical tail ending in a bunch of cilia. Near the apex dorsally a protrusile elevation with the genital opening surrounded by five or six cilia. No alimentary canal, only two blackish bodies situated near the base of the tail, and two bright bodies on both sides of the testis and which Joliet regards as "les glandes stomacales". A large pyriform testis containing numerous spermatozoa occupies the greater part of the body cavity; a brain is indicated with some doubt; of the excretory organ only two vibratile tags near the forepart of the animal are observed. A few muscles are detected.

WEBER (1898, p. 288) writes

Le male atteint en grandeur à peine les deux tiers de la femelle. Il ressemble à une jeune larve de femelle. Son corps est presque cylindrique; il est terminé en avant par une tête arrondie à couronne ciliaire bilobée mais mal définie. Sa tête est nettement séparée du tronc par un étranglement. Le pied est court, conique, terminé par une couronne de cils raides. Le système excréteur est réduit; les organes digestifs absents. Les organes des sens réduits à un ganglion cérébroïde et à deux yeux. Le testicule est volumineux; le pénis est dorsal, cylindrique et terminé comme le pied par une couronne de cils. Je n'ai trouvé qu'un seul exemplaire W. has reproduced Joliet's figure (Pl. 11, fig. 6).

HLAVA (1908, p. 71, fig. 25 D) writes

Das Männchen ist dem jungen Weibchen ähnlich. Das Vorderende ist abgerundet und schwach von dem Rumpfe abgeseht; die Krone ist mässig zweilappig. Auf der Dorsalseite dicht unter dem Kronenrande sind zwei rote, mit deutlicher Linse versehene Augen gelegen. Der Körper ist annähernd walzenförmig und mit einem kurzen, konischen Fusse versehen. Am Ende desselben befindet sich ein Borstenbüschel. Dorsal an der Fussbasis ist ein kleiner



walzenförmiger, zurückziehbarer und am Ende bewimperter Penis gelegen. Verdauungskana fehlt; anstatt desselben ist ein grosser, birnförmiger Hoden entwickelt.

Size: Male 400—600  $\mu$ , female 1300—2000.

#### **Melicerta conifera** Hudson.

Hudson-Gosse 1889, p. 72.

GOSSE in HUDSON-GOSSE (1889, p. 72, Pl. D, fig. 6) supposes

that he has seen the male; but the figure and description are so sketchy that they have only very slight scientific value.

#### **Melicerta janus** Huds.

Hudson-Gosse 1889, p. 75.

HUDSON-GOSSE (1889, p. 75) writes:

"Mr. Hood tells me that he has seen the male, and that it resembles that which I have figured as the male of *M. tubicolaria*."

#### **Melicerta tubicolaria** Ehrbg.

Hudson-Gosse 1889, p. 73.

HUDSON-GOSSE (1889, p. 73, Pl. 5, fig. 3 c). HUDSON supposes

that he has seen the male. "The nervous ganglion, spermsack and penis were plainly visible, and I could see the motion of the spermatozoa, though not the individual spermatozoa themselves; neither could I make out the muscles nor the water vascular system."

The *Melicerta* colonies, especially those of *M. ringens*, but also those of *M. janus*, are very common in our ponds. Curiously enough I have never had the good luck to observe the males.

#### General remarks.

It will be seen that we possess only a limited knowledge of the males of *Conochilus volvox*, *Lacinularia socialis* and *Melicerta ringens*. The males are always small often only about 50  $\mu$ ; that of *L. socialis* 2—300  $\mu$ ; coneshaped without any conspicuous foot, but often with a cupshaped body, a sucker in which the foot glands debouch. The wheel-organ is a single ciliary wreath, encircling a disc, which is commonly cone-shaped, carrying two eyes, provided with lenses. A large brain; most probably always a dorsal and two ventral antennæ, but they have not always been observed. No mastax and often no trace of alimentary canal at all. Lateral canals with vibratile tags not always detected, but perhaps always present; no contractile vesicle. A large pyriform testis, a cilia-covered ductus seminalis, no real penis but the ductus seminalis may be partly turned inside out; large masses of oil globules. Muscular system insufficiently known; many transversal muscle bands seem to be a rule. The males are extremely active animals and very variable in form.

#### **Microcodonidæ.**

The family comprises the two genera *Microcodon* and *Microcodides*. The males are almost unknown.

**Microcodon clavus** Ehrbg.

Gosse 1889, p. 119.

GOSSE (HUDSON-GOSSE 1889, p. 119) supposes he has seen the male.

"A female had been playing in my live-box within an area formed by bounding filaments of *Myriophyllum*. Presently I saw a slender worm, about as long as this charming subject itself, of almost aerial transparency, very slender, darting about the same limited area. It was a nearly perfect cylinder, but gradually tapering to an acute extremity, which may possibly have been a minute conical toe. The front, slightly bent downward, was transversely truncate; its circular margin carrying a wreath of locomotive cilia, by whose vibrations it shot vigorously and rapidly about. The whole body was refractive of light, but one vesicle, situate about two-thirds from the front was more intensely refractive. This I suspect to have been the sperm-sack. I could detect no other organ or viscus in the animal, but the entire length and breadth was full of minute granules." Gosse further supposes that he did indeed observe the male, because the motions exactly resemble those of the female, because it appeared at the same time and in the same dip. In support of his supposition he also emphasised the apparent attention, which the supposed male paid to the female.

**Microcodides robustus** (Glascott).

Tab. VI, fig. 1—2.

Description. Body about twice longer than broad, sackformed behind; cross section almost circular. The forepart of the body rather sharply defined from the broader hindpart; cuticula thin, very hyaline. Foot remarkably strongly developed, almost more so than in the female, but only with two joints; ventrally placed two rather blunt short toes. Wheel-organ resembling that of the female, but the cilia as far as I have been able to see, form a closed wreath round the somewhat obliquely placed disc; upon this a few faintly developed elevations, carrying bunches of long cilia. Below the hypodermal cells the large brain with a red eye below. Dorsal antennæ two, situated near each other, united in a dorsal organ; two lateral antennæ far behind. There are four conspicuous transversal muscle-bands; of longitudinal bands three or four dorsal bands and two ventral ones; some of them are deeply cleft. There is a conspicuous, but rather narrow rudiment of the alimentary canal, embracing the testis; the lateral canals are very conspicuous, furnished with three vibratile tags each. No contractile vesicle has been found. The testis is large, pyriform, suspended in a very hyaline indusium of a similar structure to that which is found in *Hydatina*; there are two sorts of spermatozoa; two small prostata glands. Peculiar are the two highly developed footglands, ending at the tip of the toes. The opening for the testis is situated dorsally over the first footsegment; the penis seems to be rather short, protrusile, the opening is surrounded by a wreath of cilia. Size of female 6—700  $\mu$ , of foot 250. Size of male 160  $\mu$ .

It is only with the greatest hesitation that I refer this peculiar male to the genus *Microcodides*, but of all known Rotifers I cannot find any which it resembles more than the female of *Microdides robustus* described by GLASCOTT (1892) and later on figured and redescribed by Rousselet (1895, p. 3).

In May 1921 I found, in a little pond near Hillerød, a large, slowly swimming Rotifer with sharply defined, ventrally placed strong foot; the mastax was very pe-

cular, differing from every thing, that I have hitherto seen. In the same sample I soon found a few males; thinking that the female could be found again, I thoroughly studied the males for some days. On returning to the pond however, I was unable to find a single specimen more, neither male, nor female. In the autumn of 1921, during the whole of 1922, and in the spring of 1923 the pond was under regular observation, but all efforts were fruitless. For a time I supposed that a closer examination of the female would show that I had a *Harringia* (= *Dinops*) before me. As I am sure however, that the two dorsal antennæ are united in a single dorsal organ, and a cursory examination of the mouthparts showed no resemblance to those of *Harringia*, this was not the case. The wheel-organ of the female was quite in accordance with that of *Microcodides*, and the hindpart of the body showed the same parallel furrows which are so characteristic in ROUSSELET's figure.

### Flosculariidae.

The family comprises the three genera *Floscularia*, *Stephanoceros* and *Apsilus*, all three with only very slight mutual relationship. Of many of the species it is stated that the males have been observed, but they are neither described nor figured.

#### *Floscularia proboscidea* Ehrbg.

= *F. campanulata* Dob.

Male: Hudson 1875, p. 45.

Hudson-Gosse 1889, p. 52.

Weber 1888, p. 10.

— 1898, p. 277.

Montgomery 1903, p. 363.

HUDSON-GOSSE (1889, p. 52, Pl. I, fig. 1 c.)

The sperm sack and penis are indistinctly shown in the figure, but the dead specimen from which I drew the figure was so lately hatched that its cuticle was more than usually opaque.

WEBER (1888, p. 10, Pl. 26, fig. 2; 1898, p. 277, Pl. 10, fig. 11).

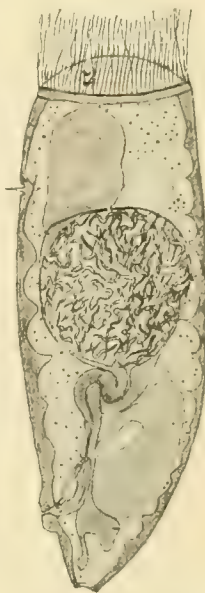
"Le male de *F. proboscidea* est rare et je n'ai réussi à en trouver qu'un seul exemplaire. Il est de petite taille et ressemble à une toute jeune femelle. Il a la forme d'un sac allongé, tronqué aux deux extrémités. Pied très court et obtus. Le sommet de la tête est très légèrement divisé en lobes et porte une couronne de cils fins et longs. Les deux yeux sont bien visibles. Le système digestif fait défaut, le système excréteur est réduit, deux canaux latéraux, commençant dans la tête et se terminant de chaque côté du pénis au dessous du pied. La majeure partie de la cavité du corps est occupée par un testicule granuleux. Le pénis est court, dorsal, muni d'une couronne ciliée à son extrémité. Le système musculaire est composé de deux forts muscles latéraux, rétracteurs de la partie antérieure du corps, la tête, et des muscles fins du pénis et du testicule."

HUDSON's observation, that the males pierce the tube, Weber (1888, p. 11) regards as highly improbable.

MONTGOMERY (1903, p. 363, Pl. 21, fig. 36). Out of the more exhaustive picture we point out the following facts.



The mature male in size and general structure, disregarding the sexual organs and the alimentary tract, shows a great similarity to the immature females. It lacks an alimentary tract entirely; M. was unable to find a nephridial system, though undoubtedly the latter must be present. The thickened hypodermal ring at the anterior end of the body bears a single ring of long, vibratile cilia, and in the projection of the trunk, anterior to this ring, lie two semicircular, dorsal, red eyes. The foot is very short, without peduncle. The hypodermis is thickened and with an irregular scalloped inner contour. A dorsal sense-organ is well developed. In the anterior region of the trunk lies a large mass, which may in part represent a cerebral ganglion. The genital organs consist of a huge sperm sack, connected with a cirrus. This sperm sack is filled with spermatozoa, and its walls thin, except at one point on its dorsal surface, which is thickened; probably this thickening represents the germinal epithelium and therefore the testis proper. A curled thick-walled tube, the cirrus, follows the sperm-sack; its lumen, the vas deferens is very narrow. A thin-walled short tube connects the posterior end of this cirrus with the dorsal genital aperture; and within this tube beat long cilia, which are attached to the posterior end of the cirrus. The cirrus may be protruded some distance out of the genital aperture, and probably serves as an intromittent copulatory organ. On the ventral side of the cirrus, in close attachment to its wall, is a large dense body, with an axial pyriform clear space, a gland; the clear space being its ductus. Just posterior to this gland is a lobed body, projecting into the body cavity, bearing on one of its surfaces long cilia, which beat in the body cavity.



*Floscularia proboscidea* ♂ after Montgomery.

### ***Floscularia calva* Hudson.**

Male: Hudson-Gosse 1889, p. 56.

HUDSON-GOSSE (1889, p. 56, Pl. III, fig. 3 a, 3 b). Hudson states:

"I am indebted to Mr. Hood for drawings of the young male and female each of which he saw hatched from egg laid in the tube. The male is about  $\frac{1}{16}$  inch in length and resembles that of *F. campanulata*."

### ***Floscularia mutabilis* Bolton.**

Male: Hudson-Gosse 1889, p. 56.

HUDSON-GOSSE (1889, p. 56, Pl. III, fig. 2 c). Hudson says:

"I have seen what I believe to be the male but I failed to isolate it so as to make out its internal organs."

### ***Floscularia cucullata* Hood.**

Male: Hood 1894, p. 335.

HOOD (1894, p. 335, Tab. XVI, fig. 3) writes:

"The male has a prominent dorsal antenna; all other males of *Floscules*, so far as observed, having no such antenna; it has also two small eyes close together."

### ***Floscularia ambigua* Hudson.**

Hudson-Gosse 1889, p. 53.

HUDSON-GOSSE (1889, p. 53) writes:

"Mr. Hood has twice seen the male, hatched from the egg, laid in the tube, and noticed the motion of its spermatozoa in the sperm-sack."

**Floscularia pelagica** Rouss.

Rousset 1893, p. 444.

ROUSSELET (1893, p. 444, Pl. 7, fig. 1 d).

"I saw a young male born; it is of usual shape with two red eyes."

**Floscularia ornata** Ehrbg.

Tab. XV, fig. 6—7.

Description. The male cone-shaped, attenuated at posterior end, but without peduncle and without any coating of gelatinous substance. The coronal disc cone-shaped, covered with a coating of short cilia encircled by a ring of long cilia but wholly destitute of the long stiff setæ so characteristic of the corona of the *Floscularia*-females. A hypodermal ring of thick, large cells, a large brain; anteriorly inside the ciliary wreath two red eyes. From the brain two antennæ running to a sharply defined dorsal organ, provided with a tuft of cilia; no lateral antennæ have been observed. No alimentary canal but before the testis a large globular body, perhaps a rudiment thereof, perhaps a large oil-globule. Two lateral canals ending near the opening of the penis, each provided with three vibratile tags; no contractile vesicle. A large testis, filled with spermatozoa; hitherto staff-formed ones have not been observed; ductus seminalis is curved, provided with cilia in its interior, and with two prostata glands laterally. At its apex a bunch of cilia; during copula the canal is turned inside out and presents itself as a dorsal conical projection, provided with a ring of cilia. Ten transversal muscle bands, which in a very high degree are able to constrict the body and alter its form; at all events two pairs of longitudinal muscle bands. Size of the male 45  $\mu$ . Size of the female 750  $\mu$ .

The male eggs were found in the tubes; for some time the males are in the egg shell; then for a short time they swim round in the tube of the female where upon they leave the tube; during the few hours they live, they do not seem to leave the female colonies, always encircling the coronas and upper part of the tube.

**Stephanoceros Eichhornii** Ehrbg.

Male: Western 1893, p. 157.

Dixon-Nuttall 1897, p. 166.

WESTERN (1893, p. 157) states that HOOD is the first who has seen the male and later on sent him females with male eggs in the tubes (April).

"The eggs were laid in batches of three or four, some two or three hours before the young males emerged from them. . . . After birth the young males, measuring about  $\frac{1}{180}$  in., were within the tube, and from it I distinctly saw two or three of them bore their way out through the side, leaving in one case a hole with ragged edges. This process took them six or eight hours. . . . There is a sort of head with two red eyespots. This is surrounded by a ciliary wreath, of which the cilia are very long and active. Below this the body gradually

tapers to the foot. There are two antennæ, to which as to the eye spots, nerves could be traced from a largish square-shaped ganglion in the neck. The sperm-sack occupies the lower half of the body cavity. There is also a small contractile vesicle, and the lateral canals, with at least three vibratile tags on each side, are easy to make out.

DIXON-NUTTALL (1896, p. 166, Pl. V, fig. 1—2).

"Like most male Rotifers they are restless and swim about in an apparently aimless manner. The dorsal antenna is situated on a small hump, and at each side of it lie the lateral antennæ. In some animals these are furnished with a bunch of long fine setæ, though in several examples that I looked at most carefully I was unable to find them; it is possible they may get broken off. The many celled sperm-sack (in which may be seen the spermatozoa actively lashing their flagella) takes the place of the stomach and intestine. The vascular system, with its contractile vesicle, is normal. The corona is circular, and furnished with a wreath of fine vibratile cilia; the front of the head is conical, and two red eyes rather wide apart, are conspicuous.  $\frac{1}{90}$ — $\frac{1}{60}$  inch.

WEBER (1898, p. 282) has observed the male.

I have only found *Stephanoceros Eichhornii* once in Gudenaa near Silkeborg and never seen the male.



*Stephanoceros Eichhornii* ♂  
after Dixon-Nuttall.

### *Apsilus lentiformis* Metchnikov.

Male: Metchnikov 1866, p. 354.

METCHNIKOV (1866, p. 354, Tab. 19, fig. 4). Abstract:

"Form conish, nach hinten zugespitzt; Kopfwimperapparat besteht aus einem geschlossenen Ring von langen Flimmern; am Hinterende noch eine Anzahl auf einem abgesonderten Zapfen sitzender Flimmerhaare. Cuticula dick; darunter eine Anzahl vereinzelter Zellenkerne. Ein grosses Hirnganglion mit zwei Augen von rothen Pigmentflecken und einem Krystallkörper zusammengesetzt. An beiden Seiten des Gehirns zwei besondere Gefühlsorgane von birnförmiger Gestalt; sie tragen auf ihrem vordern äusseren Ende je ein Knöpfchen mit einem davon auslaufenden feinen Härchen; das hintere Ende dieses Organs, welches vielleicht einer spindelförmigen Nervenzelle entspricht, geht in einem dünnen Nervenfasern über. Ringsum Längmuskeln, welche von einzelnen Fasern gebildet werden, die sich dadurch auszeichnen, dass jede nur aus einer Zelle besteht, und je einen hellen mit einem Nucleolus versehenen Kern enthalten. Keine Verdauungsorgane. Excretionsorgane vorhanden: Eine contractile in die Geschlechtsöffnung einmündende Blase und zwei seitlichen, von dieser ausgehenden Gefässen; jede tragen drei Trichter. Testis unpaar; besteht aus einem aus Zellen zusammengesetzten Teil und einen untern mit reifen Zoospermien erfüllten grössern Behälter. Von letzteren entspringt ein ziemlich langer Samenausführgang, welcher an der Spitze des Penis ausmündet. Dieser stellt einen aus- und einstülpbaren Zapfen dar an dem ein Bückel ziemlich starker Flimmerhaare aufsitz. Zweierlei Zoospermien. Hinten einen aus feinkörnigen Inhalt bestehende Drüsen (Prostata). Grosse 0,28."



*Apsilus lentiformis* ♂ after Metchnikov.

### General remarks.

The males of the Flosculariidae are very insufficiently known. Hitherto only the male of *F. campanulata* has been fairly well described (MONTGOMERY); further the rather peculiar male of *Apsilus* hitherto only found by METCHNIKOV.



As far as we hitherto know, all the males of the *Flosculariidae* are freeswimming animals, without gelatinous tube, cylindric or cone-shaped; no peduncle; it is doubtful if there exists a sucker, by means of which the male may fasten itself to the female; something in this direction may perhaps be interpreted in this way in the figure of MONTGOMERY (fig. 36 x y). In the male of *Floscularia ornata*, I could find nothing of that.

The coronal disc is always placed vertically, covered with a rather uniform coating of short cilia and encircled by a simple wreath of cilia; no setigerous lobes or long setae have ever been observed in a male of the *Flosculariidae*, and as the whole alimentary canal is absent, there is not the slightest trace of the highly specialized vestibulum, so characteristic of the female. All species present two red eye spots, placed on the cone-shaped disc. From brain conspicuous nerves are given off to a dorsal organ, which is most probably always present; whether the same is the case with the lateral antennae is doubtful; hitherto they have only been observed in *Stephanoceros* and in *Apsilus*. The alimentary canal is wholly absent, a rudiment as a suspensor testis perhaps present. Excretory organs present as two lateral canals with a series (3—4) of vibratile tags; they have only been observed with certainty in *Stephanoceros*, *Apsilus* and *Floscularia proboscidea* (by WEBER) and in *F. ornata* (by myself); the contractile vesicle is supposed to be present in *Stephanoceros* and in *Apsilus*.

The testis is always large, pyriform; whether it always contains two sorts of spermatozoa is rather doubtful, pointed out in *Apsilus*; the ductus seminalis is short, now and then curved, coated with cilia inside, opening dorsally. There is no real penis but most probably during the mating process the last part of the ductus seminalis is turned inside out. Prostata glands are always present. A long series of transversal muscle bands and strong longitudinal muscles.

The males are hatched in the tubes of the females and their freeswimming period most probably very short.<sup>1</sup>

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## Chapter IV.

### Anatomical Remarks Relating to the Males of the Rotifera.

In the following lines I have tried to give a sketch of the structure of the males of the Rotifera. With regard to some of the organs, this is only possible with full consideration of the same organ in the female sex. When this is the case, the description has been begun with a more general survey of the organ in this sex, laying weight upon just those points which are of significance for the understanding of the structure of the same organ in the male sex.

<sup>1</sup> ROUSSELET (1903, p. 174) states that THORPE has found the male of *Trochosphaera æquatorialis*; with regard to the very aberrant males of the *Seisonacea*, I refer the reader to the papers by PLATE and CLAUS.

The body of the Rotifera females is commonly described as consisting of three parts, an anterior part carrying the wheel-organ and mouth and enclosing the brain and retrocerebral organ, the middle part containing the viscera, and finally the foot. It is covered by a cuticula which, in the middle part, is often thickened to a lorica in which head as well as foot may often be drawn in; where a lorica is wanting, the body is commonly more or less segmented or as in the sessile families, where the three main parts of the body are not distinctly separated from each other, highly contractile. Besides, the body of the females is characterised by the most extraordinary variation, relating to the shape of the body, the form and composition of the lorica, the thickness of the cuticula, the development of the foot, and the shape of the disc and the wheel-organ. This great variation is developed in a much slighter degree in the males of the Rotifera.

Firstly sessile male Rotifers are hitherto wholly unknown and most probably do not exist, all males belonging to sessile females being conical without any conspicuous differentiation of the body; the cuticula is always extremely thin, much thinner than in the female and therefore also very hyaline. In the more primitive families, as especially the *Notommatidæ*, where the body is conspicuously segmented and more or less telescopic, the segmentation in the males, especially in *Diglena*, in some species of *Notommata*, and perhaps also in *Copeus*, is often rather obvious, but the telescopic power is much smaller; f. i. *C. labiatus* and *C. pachyurus* in the female sex can telescope themselves in such a way that the body is ballshaped, whereas this is not the case with the few males I have seen. In many cases, especially where there is no lorica, the body of the male is almost a true repetition of that of the female, the body being only much smaller, commonly only one third of that of the female. This is the case with the males of *Hydatina*, *Rhinops*, *Notops brachionus*, partly also with those of *Synchaeta*, and some of the *Notommatidæ* f. i. *Diglena*. Here it is interesting to see how the shape of the males is in accordance with the shape of the female; the thinner the female is, the thinner too is the male. This is also the case with the *Asplanchnas* where the male of the broad ballshaped *A. Brightwelli* and *A. Sieboldi* is also ballshaped, whereas the male of *A. priodonta* is oblong.

On the contrary especially in the plancton Rotifers where the size of the male is very much reduced, there is not the slightest resemblance between the shape of the two sexes. To these, the most reduced of the Rotifer males, we shall return later on.

As well known the skin of the female Rotifers consists of an extremely thin protoplasmatic layer, a syncytium without cell limits and with relatively few nuclei. It is covered with an often very thin cuticula which, when thicker, is termed a lorica. In the males the protoplasmatic layer is commonly still thinner, and the cuticula so thin and hyaline that the males f. i. those of the *Asplanchna*-species resemble crystalline bubbles. On the other hand some of the males are very opaque so that it is almost impossible to see the interior organs. This is the case with the males of *Salpina*, of *Metopidia*, the *Gastropus* species and others. Most probably this is due to a thick hypodermic layer; the males in this regard resembling the newly

born females which only attain hyalinity during growth. In the few cases where I have been able to observe the longevity of the males (*Asplanchna*, *Hydatina*) I have seen that the males, too, are more transparent in the last part of their life and that just these males grow larger during the few days they live. The greater hyalinity is most probably due to the spreading out and flattening of the hypodermic layer behind an always increasing surface; this will especially be understood when we remember that the males get no food during life.

If the body of the female is covered with a lorica, the lorica of the male may in some and relatively few cases be a true picture of that of the female; this is the case with the lorica in the hitherto known specimens of *Salpina* and *Euchlanis* perhaps also in *Metopidia*. In those species in which we commonly do not speak of a real lorica but in the cuticula of which we find characteristic keels and furrows f. i. *N. hyptopus*, we find this system again in the male.

In the great families of loricate Rotifers: *Brachionidae* and *Anuraeadae* in which the lorica in the female reaches almost its highest development, we can hardly speak of a true lorica in the males; there exists a rather thick cuticula, provided with some conspicuous and constant keels and furrows which are not as a rule in accordance with anything in the structure of the lorica of the female; the facettation of the lorica which is so highly characteristic of that of many of the females, is here wholly wanting.

This lorica is further characterised by the peculiar, commonly strongly developed spines at the anterior and posterior ends; we do not know any equivalents to these spines in the males. It is a peculiar fact, that the males of the Rotifers even if the females have highly developed spines, hardly ever possess spines of any kind. Apart from the *Brachionidae* and *Anuraeadae*, this also holds good for the *Triarthra* and *Polyarthra*, further for all the hitherto known males of *Rattulidae* and *Dinocharidae*. We only meet with spines similar to those which we find in the lorica of the females, in the *Salpinidae* and in the peculiar spiny process on the head of *Colurellidae*. Where the lorica presents peculiar structures in the female sex, these peculiarities are absent in that of the males; we have in the males no facettation of the lorica and no anterior ring of plates in the faintly developed lorica of *Dinocharis* (WEBER) and no hint of the peculiar foam-like structure of the lorica of *Ploesoma hudsoni* ♀. Further we never find any trace in the males of that peculiar yelly envelopment so characteristic of the female of *Copeus labiatus*.

**Foot.** Female sex. Especially among the creeping Rotifers with ventrally situated disc the foot is not sharply separated as a special organ from the other part of the body. It consists of from two to four "segments" which are feebly telescopic; on the last "segment" it carries two toes which are provided each with a foot gland. By means of sticking material from these glands the animals are able to fasten themselves to a substratum. A foot of this structure is designated as a creeping or crawling foot and is mainly found in the *Notommatidae*; by means of the sticking material from the foot glands the animals now and then fasten themselves to the



substratum; many of them are really mainly sedentary animals. The more the Rotifers pass over to a swimming motion, the more the foot loses its importance as a creeping organ; it is now mainly used partly as a steering organ partly as an organ of attachment. In accordance with the first named function, but in very different ways, it is now almost always conspicuously separated from the other part of the body; only in the *Synchaetadae* where parts of the wheel-organ (the auricles) play the rôle of steering organs, the foot is the typical foot of the creeping Rotifers now only used as an organ of attachment.

In the freeswimming Rotifers the foot has a very different shape but is often formed in accordance with its main function of steering organ. This for instance is the case with the foot in the two families *Salpinadae* and *Euchlanidae* where it may be shown how the broad toes are used; this is also the case with the annulated foot of *Pterodina*, *Ploesoma*, further with many of the *Brachionidae*, where the foot is only used at the special moment when the direction of the movement is to be greatly altered; during the slowly rotating motion, the foot is often withdrawn into the lorica, especially in one of the most pelagic species *B. pala*. Still it preserves its significance as an organ of attachment. In many of the plancton Rotifers the foot glands either atrophiate or are feebly developed.

Very many of the true plancton Rotifers have no foot at all; they are therefore unable to attach themselves (*Asplanchna*, *Triarthra*, *Polyarthra*, *Pompholyx*, *Pedalion*, *Anuraea*, *Notholca*, *Ascomorpha*, *Anapus*) and if not provided with leaping thorns unable suddenly to alter the direction.

Even if the foot disappears, it is not quite certain on that account that the foot glands also disappear. Many of the plancton Rotifers carry their eggs glued to the posterior part of the body, in *Pompholyx* fastened by a peculiar system of threads, which can be pushed out and in from an apical opening. Further investigations will show if the glutinating matter is derived from rudimentary foot glands which have undergone a change in function.

Among the slowly swimming inhabitants of the small ponds, covered with carpets of leaves, and those from the pelagic region of the lakes, with regard to the reduction of the foot there exists the most beautiful series of reductions (e. g. *Hydatina*, *Notops brachionus*, *Brachionus*, *Anuraea*. — further *Asplanchnopus*, *Asplanchna Herricki*: *Asplanchna priodonta*. — Species of the genus *Synchaeta* and of the *Ploesomatidae* show other examples in the same direction. — Peculiar foot forms are especially found among the half swimming, half creeping, Rotifers of the ponds e. g. the jumping foot of *Scaridium*, *Dinocharis* and some *Furcularia*-species. Even if the foot among freeswimming Rotifers is used as a steering organ still it is in very many cases here also used as an organ of attachment; very many of the so-called freeswimming Rotifers are in a still higher degree than commonly supposed fixed animals, which the net has thrown off from their substratum and which live a more swimming life in the vessels than in nature. Even among the freeswimming Rotifers we often find very peculiar structures of the foot glands; these organs may develop to a very

high degree of perfection. This f. i. is the case with the *Rattulidae*. With regard to the significance of the asymmetry in the foot forms in this family I especially refer the reader to JENNING's admirable paper.

The foot of the *Bdelloidae* which is used telescopically in creeping, and withdrawn in swimming, is in many species mainly an organ of attachment and the foot provided with a series of until five pairs of foot glands, the glands lying above each other. In the moss living *Callidina* species and *Discopus* it is only used as an organ of attachment, and here provided with a sucker. Also in the *Flosculariidae* and *Meliceridae* the foot is only an organ of attachment, but simultaneously, it has here the rôle of carrying the fully distended animal back into the bottom of the tube again when contracted. In accordance herewith it is provided with long powerful muscles in fixed numbers. In the young freeswimming animals the greater part of the foot is occupied by large foot glands; later on, when the animals have fastened themselves, they atrophy. Whether the peculiar stick-like appendages of *Pedalion* may morphologically be regarded as parts of the foot is doubtful.

Foot, male sex. If we will now try to take a survey of the different foot forms in the male sex, it will soon be obvious that the differences here are by no means so great as in the female sex. In the most primitive family, the *Notommatidae*, the foot in the two sexes is almost of quite the same structure. It is also used quite as in the female as a creeping organ and because the foot glands are always well developed, also as an organ of fixation. In the males of the *Synchaeta* the foot and foot glands are much more reduced than in the female sex, the organ being here a true appendix to the penis. In *Hydatina* and *Rhinops* it is well developed, reduced in *Notops brachionus*, and still more in *Brachionus*; the foot is here not retractile as in the female sex; it is short and thick, is never used as a steering organ and only for attachment. Very often the *Brachionus* males swim with the enormous penis fully evaginated and with the foot then hanging downwards as a small ventral appendage. In the *Anuraea* there is no foot at all either in the male or the female sex; at a first glance it looks as if the males are provided with a long fleshy appendix that looks like a foot; this is however only the long penis which, especially in *A. hypelasma*, is flexible and is used in some way as a steering organ during the swimming motion. It is always protruded. In *G. hyptopus* the foot in the male sex is very inconspicuous and always carried retracted; only during the copulatory act it is protruded together with the penis, then hanging downwards as a small inconspicuous appendage. In *Gastropus stylifer* the female sex has a remarkable narrow foot without toes while in the male sex it is reduced to a very inconspicuous styliform process, but provided with a comparatively large foot gland. In some genera in which the female has a foot (*Ploesoma*, *Rattulus*) the foot in the male sex is wholly wanting, and in all those genera where the female sex has no foot at all, it is also absent in the male sex. As regards the freeswimming Rotifers, where the foot is used as a steering organ, it is only among the *Euchlanidae* and *Salpinadæ* that it is used in that way also in the male sex where it is used as a leaping organ in the female

sex (*Dinocharis*, *Scaridium*), it is reduced to a simple swimming organ in the male sex. As the males of the fixed Rotifers, the *Meliceridae* and *Flosculariidae* are always freeswimming organisms, never living in tubes, the foot of these species is not provided with all those peculiarities which characterise the female foot in these families, and which help the females to sink down in the protecting tube. All in all it will be understood that the foot in the male sex is a much more reduced organ than in the female sex. As a swimming organ it has lost its significance in many families; but it has preserved its significance as an organ of fixation. In accordance herewith the foot glands only rarely disappear. The substratum upon which the males mainly use the foot is the body of the female; therefore it has mainly significance during the mating process. It disappears for the benefit of the development of the penis which is partly formed by means of blood pressure upon the dorsal side of the foot.

Wheel-organ. Female. As mentioned above the wheel-organ of the Rotifera was formerly interpreted as consisting of two zones of cilia, the inner one termed trochus the outer termed cingulum, both encircling a circular funnel and with a finely ciliated groove between them. This is the interpretation of LEYDIG, HUXLEY and PLATE. This view was adopted as late as 1910 (HARTROG). As mentioned above already METCHNIKOV and JOLIET, later on myself and lastly DE BEAUCHAMP have tried to show that the original wheel-organ of the Rotifera is really a ventrally situated ciliated disc ("la plaque ciliée buccale" DE BEAUCHAMP). In the most primitive types (some of the *Notommatidae* and the *Adinetidae*) this ciliated disc without any bordering zone of longer cilia is still preserved. This ciliated plate is simultaneously an organ of locomotion with which the animal moves slowly over the substratum, partly an organ with which the food is brushed off into the mouth; the organ cannot be used for swimming, and the animals creep in Turbellaria-manner over the substratum. As the Rotifera accustomed themselves to the swimming motion, the cilia at the borders of the disc were forced to overcome a much greater resistance than those covering the centre of the disc. The result was the development of the bordering zone of cilia, the "bande circumapicale" DE BEAUCHAMP. In the most primitive types this band is in the main only developed in quite particular lateral parts of the disc, and these parts, the so-called auricles (oreillettes) or "Wimperöhren", are then capable of being withdrawn and extended again. When withdrawn, the animal is still a creeping, when protuded, a swimming animal (many *Notommatidae*). They are especially well developed in those families where the foot is not well marked off from the other part of the body, and preserved in those swimming families where the foot cannot therefore be used as a steering apparatus, the auricles being used in this way (some *Notommatidae*, *Synchaetidae*).

Simultaneously with the development of a wheel-organ, consisting of a ciliary disc, bordered by a more or less continuous row of longer cilia, the position of the disc is altered from a more ventral to a more vertical one. The more the animals



emancipate themselves from a substratum and pass over to being strongly freeswimming animals, the more vertically is the wheel-organ placed. In the families of the *Notommatidæ*, in the developmental series *Hydatina*, *Rhinops*, *Notops brachionus*, and the *Brachionidæ*, we find excellent examples of this phenomenon. A wheel-organ of these hitherto mentioned types is really a swimming organ, but has no importance as an organ by means of which the nourishment may be seized. This is only done by means of the mouth parts, which are near the mouth opening, and are often capable of being protruded as catching organs. Very many of the wheel-organs of the freeswimming Rotifers are really modifications of this very type.

The more the animals pass over to being freeswimming individuals, quite emancipating themselves from a substratum, the more often is the disc, in accordance herewith, placed terminally. The homogeneous cilia-covering of the disc disappears, giving place to elevations of different kinds, hills, plates, etc., covered with much stronger cilia; simultaneously herewith the bordering band of cilia of the disc, commonly reduced in the middle line dorsally and ventrally, is more strongly developed, and great parts of the disc itself may be quite destitute of cilia. In different ways the strong cilia of the disc planted upon small elevations, hairpads are of significance as stopping apparatus for the catching of prey; but still the mouth parts play a prominent part in this way. Wheel-organs of this type we meet with in the *Euchlanidæ*, *Salpinadæ*, *Coluridæ*, *Cathypnadæ*, *Dinocharidæ*, *Ploesomatidæ*, *Gastropodidæ*, *Rattulidæ*, *Hydatinidæ* and *Brachionidæ*. Almost all these Rotifers belong to smaller ponds rich in plants and whose surface is divided by means of floating leaves in innumerable small pelagical regions in which most of these animals live their lives, half swimming, half creeping, often fastened to the leaves. Many of them are typical vegetarians, gnawing the diatoms coatings etc. upon the leaves, most of them get their food when, half swimming half creeping, they move over the substratum using their wheel-organ mainly locomotorically; the most elaborate forms are really plancton organisms, inhabiting the pelagic regions in ponds, pond lakes and exceptionally also real lakes. As such may mainly be mentioned most of the *Brachionidæ*, and a few *Gastropodidæ* and *Ploesomatidæ*. In the *Brachionidæ* the wheel-organ, in accordance with its structure, is used as well locomotorically as for the catching of nourishment; in the two last named families mainly locomotorically, the mouth parts being here used as organs which catch the prey when the animal crosses its way through the water layers. In one of the most typical groups of plancton Rotifers the *Asplanchnadæ* the ciliary disc is quite destitute of cilia, a wreath of cilia encircling the nude disc, only provided with some tufts of cilia with sensorial functions; but also this wheel-organ is only locomotive, the prey being caught with the mouth parts during swimming.

In case the wheel-organ in freeswimming or sessile Rotifers is to act simultaneously as an organ fitted both for locomotion and for provision of food, two ciliary wreaths, separated from each other by a cilia covered furrow, are developed. The material caught by the wheel-organ is carried down into the furrow between the

two wreaths, and conveyed further to the mouth. In this case the mouth parts have no significance or only a slight significance for catching the food, and do not reach the mouth opening; in some families they are far removed from it. It reaches its highest development in *Pedalion* among the plancton Rotifers and in the *Meliceridae* among the sessile Rotifers. In some of the plancton Rotifers such as *Triarthra*, *Pompholyx*, *Pterodina*, it is only faintly developed. Below the ciliary wreath there is here a faintly developed furrow, covered with very fine cilia, but this space is not limited here by a lower ciliary wreath. To this type also belongs the wheel-organ of the *Philodinidae* built in another way, but also destined to be used simultaneously for locomotion and for gathering nourishment. In many of the almost sessile moss-*Philodinidae* it is used almost exclusively in this way; here its significance as a locomotory organ is almost lost. This is also the case with the wheel-organ in some of the above-named types, some of them being almost sessile organisms; this f. i. is the case with many of the *Brachionidae* which, once fastened to a substratum, only very rarely leave it. (*B. rubens* upon Daphnids). By means of a peculiar structure it obtains significance also as a tube forming organ in some of the *Meliceridae*. A very peculiar wheel-organ occurs in the *Flosculariidae* which can only be understood on the view that we have here organisms which are simultaneously sessile and animals of prey (DE BEAUCHAMP). The disc is here formed like a funnel whose borders commonly taper into lobes and arms which carry long stiff cilia. Centrally at the bottom of the funnel lies a second chamber, the vestibulum, encircled by a horse shoe-shaped ciliated rim, and in the base of the vestibulum is a long slit, the buccal orifice, bounded by two chitinous lips. Organisms which have got into the funnel, cannot get out because of the long bristles which extend over its orifice; when victims enough are gathered in the vestibule they are swallowed down into the alimentary canal.

Wheel-organ, males. If we will now try to understand the wheel-organ of the males we must remember that apart from a few rather doubtful exceptions, it is only an organ of locomotion and has nothing to do with procuring food. The alimentary canal is obliterated or rudimentary and the animal gets no food whatever.

It must further be remembered that, whereas the females of the Rotifera, when swimming, mainly move along a screw line, the males mainly move along a straight line. As far as I understand, when the animals are moving along a screw line it is most probably impossible to steer towards a definite point, especially when this point is moving. They are unable to follow a moving prey or a rotating female. We therefore see that the few plancton-Rotifers which in the female sex live on other planktons which are seized and sucked out, f.i. *Ploesoma Hudsoni*, in the male sex really often follow straight lines, at all events when they are in pursuit of prey. With regard to the males of the Rotifers which are always in search of the females during their short life time it would be almost impossible for them to find and reach a female when discovered, if the motion were only rotating. It is in accordance with this that the males almost

always dart off in straight lines or in large circles, but during this motion they do not as a rule rotate round themselves.

It will further be understood that an organ of locomotion destined to move the organism along a screw line cannot be formed like one which is to move it along a straight line. I suppose that a rotating motion is mainly dependent first upon a strong development of a ciliary wreath, sharply defined from the nude coronal disc, and secondly upon the wheel-organ being placed terminally; if this is not the case, and it is nevertheless to be used as a rotating organ, the oblique position of the wheel-organ must be counterbalanced in some other way. Wheel-organs consisting of a cilia-covered disc with no stronger development of a special wreath of cilia is not an organ well fitted for rotation.

In the above-named rather cursory remarks with regard to the use of the wheel-organ in the Rotifera I have endeavoured to point out some of the main conditions for the understanding of the differences between the organ in the male and the female sex.

It must firstly be emphasised that the wheel-organ in the male sex is placed almost terminally, very rarely ventrally, and even more terminally in those species where it is more or less ventral in the females. This is in accordance with the fact that the part of the wheel-organ surrounding the mouth and which is the most ventrally placed part is obliterated in the male sex. This is especially the case with the hitherto known males of *Notommata*, *Copeus*, *Diglena* and partly also with *Hydatina*. The disc is very often vaulted, it may be flattened, but very rarely funnel shaped. It is very often covered with a coating of cilia, almost of the same length and in many cases the ciliary wreath round the disc is but slightly developed. It is just the wheel-organ which we should expect in animals which are incapable of constant rotating movements during the swimming motion. A terminally placed, almost totally nude, flattened disc encircled by a wreath of cilia we only find in the *Asplanchna*-males and just these males rotate during swimming as well as the females. Where auricles exist in the females, they are commonly not present or more slightly developed in the male sex. In the *Synchaetadæ* I have not been able to trace them; and in the many figures of *Synchaeta* which ROUSSELET has given, they are also absent; in *Ploesoma Hudsoni* they are but faintly developed, and occur only in the male sex in some males of the genera *Copeus* and *Notommata*.

From the ventral part of the disc no special part is set off as a cilia-covered furrow, almost always developed in the female, and here leading down to the mouth. It is only well developed in the males of *Rhinops* and partly also in *Euchlanis*, at all events in *E. dilatata*.

As mentioned above the disc in the female very often carries elevations of different kinds and on the tops setæ varying in numbers and size in the different species. Common to all these hair structures is the fact that in the females they are arranged in relation to the mouth; they play a rôle either as sense organs or more directly as organs for capturing the prey; they serve as a means of procuring



nourishment. In the males these hair structures are in a few cases arranged as in the females. This is especially the case with *Rhinops*, where in my opinion the wheel-organ of the two sexes is almost identical also in *Euchlanis* and in *Hydatina senta* we find a similar though somewhat simplified arrangement; where the mouth lies in the female, there is a cilia-covered spot, surrounded by hairpaths very similar to those in the females. In very many cases, especially in the most rudimentary males, the whole wheel-organ consists of some bunches of long bristles standing upon a disc, homogeneously covered with very short cilia and encircled by a wreath which is more or less sharply set off from the coating of the disc. It is a wheel-organ which is quite unable to catch any organism destined for food and which has only locomotory significance.

No males have hitherto been described with two bands of cilia round the disc. In the males of *Pedalion* and in the *Meliceritidæ* there is not the slightest trace of either a furrow or posterior band of cilia so characteristic of the females; in the males of *Pterodina* and *Triarthra* no fine coatings of minute cilia below the corona are observed, and in the males of the *Flosculariïdæ* we find nothing which may be compared with the highly elaborated wheel-organ of the females; no stiff setæ are observed; all that we find is a simple somewhat vaulted terminal disc, encircled by a single uninterrupted band of cilia equally long. It is of great interest to see how the typical wheel-organ of the Rotifers, a cilia-covered disc encircled by a single band of cilia is improved in very different ways and in accordance with the use of the organ, in the two families, the *Meliceritidæ* and *Flosculariïdæ*, and in the two sexes of both. In both families as the animals are sessile in the female sex the organ is here almost exclusively formed and used for catching food, but in the two families one of them being detritus-eaters, the other, the *Flosculariïdæ*, true beasts of prey catching the single organisms which arrive in the funnel-shaped corona and later on lacerating them with their teeth, the wheel-organs are as differently developed as possible. In the male sex in both families and where they play no rôle for procuring food and are only organs of locomotion, they are improved in very different ways from what is the type for the females. However differently the wheel-organs may be developed in the females of the two families, in the males they are of quite the same structure, formed as simply as possible, a ciliary disc encircled by a single, uninterrupted row of cilia; all those structures which in the wheel-organs of the females play a rôle for procuring food, and in the two families develop in very different ways, are here totally absent.

We are therefore able to conclude that all those different structures, which in the female sex play a rôle for catching the prey, are absent. On the other hand as the males must be more active in their movements than the females and be able to follow them, stress is laid upon improvement of the organ as strongly locomotive.

In many cases we find hairs of unquestionably sensitive significance upon the disc. In very many cases e. g. in the *Synchaetata*, *Brachionidæ*, *Anuraædæ* and others we find quite the same arrangements of these hairs in both sexes; also the fleshy

digitiform processes which are found in the females of *Ploesoma*, *Gastropus*, *Rattulus*, we find again in the male sex.

Only rarely do we find organs which do not occur in the female sex on the disc of the males. This is however the case with the genus *Triarthra*, and with some, perhaps almost all *Meliceridae*. The disc here carries a peculiar hill; where it exists it always carries the two red eyes, which in this way are brought beyond the wheel-organ and not, as in the females, concealed on a level with it.

A very peculiar organ is the so-called retrocerebral organ, which was formerly described as "Kalkbeutel" ("brain mass" HUDSON-GOSSE) and which has been studied by very many authors. It is justly due to DE BEAUCHAMP, that we now have a more thorough comprehension of this organ which is unquestionably the most enigmatic in the Rotifera. Still, there are very many unsolved questions connected with it, especially its physiological significance is still almost wholly unknown. DE BEAUCHAMP has found it in 15 of the 27 families; B. supposes that it really has existed in all families and regards it as a regressive organ, which has disappeared in the *Meliceridae* and *Seisonacea*. It consists of a retrocerebral sac, flanked by a commonly double subcerebral gland; the organ opens inside the wheel-organ with two openings, often placed upon a pair of protuberances; these openings are however very difficult to observe; the organ shows a peculiar correlation with the eye-spots, the unpaired eye being always in contact with the sac and the brain; in those species in which we find paired eye-spots, these are always placed very near the openings for the organ. It may be regarded as a glandular invagination of the ectoderm, situated in the nonciliated part of the apical zone of the wheel-organ. With regard to its significance the organ may mainly be regarded as a secretory one; it is highly probable that the two parts of the organ have not the same significance, that it is by no means the same in the different families and that its development and structure in the same species may differ from specimen to specimen, and be of different development especially at different ages. The organ is best studied in *Euchlanis*, where DE BEAUCHAMP has shown that the contents of the median sac are transformed into vacuoles, which are expelled through the orifices, after which the sac shrivels up to a much smaller circumference. Whether this emptying of the sac is a process taking place at regular intervals or only under special outer or inner conditions we do not know. In *Notommata* the secretory activity is by no means so large. In the so-called "bourses à calcaire" the secreted matter is designated as bacterioïdes, regarded as an excretion "un dépôt dans certaines cellules de produits destinés à être éliminés lentement ou à rester là jusqu'à la mort de l'animal (DE BEAUCHAMP 1909, p. 174). In the *Euchlanidae*, where we have a secretion, the secreted matter was formerly regarded as a poison. DE BEAUCHAMP supposes that it plays a rôle in the action of the cilia, perhaps that of lubricating organ and remarks that it is best developed in creeping Rotifers. In my opinion this is a very essential point. The organ is inherited from the Turbellaria as mentioned by DE BEAUCHAMP "la similitude d'une glande subcérébrale avec certaines glandes muqueuses à col très allongé et réduit

à une trainée de sécrétion comme on en connaît chez les Tricladés, les Néomériens etc. est indéniable." The more the Rotifers passed over to being either freeswimming or sessile animals and, in some of their most aberrant forms, real plancton organisms, the organ lost its significance and was gradually reduced.

The retrocerebral organ in the males has hardly ever been studied. As far as I know, it is well figured only by DIXON-NUTTALL (1892—94, p. 333, Pl. XV), but he regarded the whole organ as the brain. It would have been of the greatest interest if the investigation of the males could have brought anything special to light with regard to this organ, its structure or its significance. This is however not the case, staining methods of living animals not having been used. Owing to the slight size this will always be very difficult but is surely possible for some of the largest males of *Hydatina*, *Euchlanis* and *Copeus*. It is of interest to see that in the two genera *Euchlanis* and *Copeus*, where the organ is most strongly developed in the female, it is also strongest in the males. It has also been observed in the males of the other *Notommátidæ*, and when it has not been figured and mentioned in the descriptions of the other males, much stress must not be laid upon that point. I think that more elaborate investigations will establish its existence. In the males of *Euchlanis* and *Copeus* I have found it to be of exactly the same structure as mentioned by DE BEAUCHAMP for the females. Only I have been unable to see the Bacteroides in the median sac in the last-named genus, but that is perhaps more accidental. In the figures of *Euchlanis* I have not ventured to draw the protuberances provided with the opening. On material from Esrom lake in October 1922 I however found very conspicuous protuberances, corresponding exactly to those figured by DE BEAUCHAMP.

Alimentary canal. In its most complete shape the alimentary canal consists of eight parts in the female sex.

1. Vestibulum, which is only a depression in the disc of the wheel-organ.
2. The Pharynx or Mastax, one of the most peculiar organs of the Rotifera
3. an oesophagus covered with Cuticula and only regarded as a prolongation of the Mastax.
4. an oesophagus covered with cilia.
5. The gastral glands commonly in a number of two.
6. The ventricle formed by a single cell-layer; the cells are often arranged serially and separated from each other by means of muscle fibres; they are almost always covered with cilia and contain stored nutriment or excreta.
7. The intestine, often indistinctly separated from the ventricle.
8. The rectum, in which the excretory organ debouches; often it acts as vesica.

Even in the female sex all these eight parts are only rarely developed. The oesophagus is extremely short in the *Euchlanidæ*, the intestine is absent in the *Seisonidæ*; rectum and anus in the *Gastropodidæ*, *Asplanchna*, and *Paraseison*. Apart from the different forms of mastax, also the other parts of the alimentary canal shows the greatest possible variation in the different families.

As well known, the alimentary canal is almost always rudimentary in the male sex, does not function, and in many cases it is impossible to show only the slightest trace of it. Like other rudimentary organs, its development even in the same species



differs from specimen to specimen, and in its rudimentary form it undergoes a change of function.

A fully developed alimentary canal we only find in the male of *Rhinops vitrea* and in *Notommata Werneckii*. It is a question if really the male of *Rhinops* takes food, at all events I have never been able to see an anus or a defecation; it is further a very peculiar fact that the alimentary canal is very rudimentary in its nearest allies, *Hydatina* and *Notops brachionus*, further that it is also lost in all the primitive Rotifers, only excepting *N. Wernecki* and in all other freeswimming Rotifers. With regard to *N. Wernecki* it is perhaps a question, if the mouth parts are not mainly used to bite holes in the algæ; but having never seen this rare animal, I have no opinion about this matter.

In all other Rotifer males the alimentary canal does not function; a mouth opening never exists, and also the mastax is absent. In the place where the alimentary canal is to be found in the female, there is commonly a long broad band, which with its posterior end embraces the testis and with the other is fastened to the hypodermic cells of the wheel-organ. This band in a few cases carries a peculiar bulk like body in its anterior part immediately below the wheel-organ, in *A. priodonta* it is of a remarkable form like a parrot's beak. In *A. priodonta* it is not always present, at all events not equally developed; it is further found in the males of the two *Salpina* species which I have seen; it contains no chitinous mouth parts, but nevertheless I regard it as a rudimentary mastax. In a few cases we find two organs on the side of the band which are regarded as rudimentary gastral glands. Especially in *A. priodonta* it looks as if the band contained vacuoles, but more thorough investigations on this point would be desirable. Also in the *Synchaeta* males it looks as if the band was hollow. In very many cases it is reduced to a simple band, stretched out between the testis and the hypodermic cells below the wheel-organ; even in this form it is by many authors, with whom I fully agree, regarded as a remnant of the alimentary canal; but even this is wholly wanting in the males of many species. This for instance is the case with all the most reduced males, those of *Triarthra*, *Polyarthra*, *Pedalion*, *Conochilus*, *Pompholyx*, *Rattulus*, but also of many others which are not so much reduced f. i. *G. hyptopus*, *G. stylifer*. How sporadic and capricious the occurrence of the rudiment of the alimentary canal really is, is best seen in the *Asplanchnas*, where in *A. priodonta*, as mentioned above, it embraces the testis and is stretched out like a long band through almost the whole animal; in *A. Brightwelli* it has not been possible to find even the slightest trace of it, while in *A. Sieboldi* a peculiar rodlike body stretched out from the corona and hanging free in the body cavity can hardly be interpreted otherwise than as a rudiment of this organ. Where it is in connection with the testis, it may be regarded as highly probable that it is here used as a means to keep the testis in place.

The brain in the male as well as in the female lies dorsally over the alimentary canal; it is commonly pear shaped, now and then a little bifid. I have the impression that it is perhaps larger in the male than in the female sex but it is

possible that I have made the same mistake, with regard to the male sex as earlier authors with regard to the female sex, viz. the mistake of describing some parts of the retrocerebral organ as parts of the brain; the extreme smallness of the objects must here be my apology. In the *Polyarthra* male I have not been able to see any trace of the brain. Neither a peripheric nervesystem nor an oesophageal nor a pedal ganglion shown in the female sex in several species (e. g. in *Callidina* and *Discopus* by ZELINKA; in *Hydatina* by DE BEAUCHAMP and MARTINI (1912, p. 612) and in *Conochiloides* by HLAVA (1905, p. 209) have been found in the males; but the necessary methods of investigation have not been used.

**Sensitive organs. Female.** As mentioned above the most typical sensitive organs of the Rotifers are two pairs of tactile organs, the anterior and posterior lateral organs, which are connected by long nervethreads either directly with the brain or with peripheric ganglia-cells, lying laterally to the brain.

Only in a few cases both the two anterior and two posterior lateral organs are far removed from each other. This is the case with *Asplanchnadæ* and *Apsilus*, and they are then connected with each other by means of a transversal commissure; in the *Synchaetadæ* the two anterior ones meet each other, but in most of the Rotifera they coalesce to a single so-called dorsal organ, or dorsal antenna. Commonly two nerves are present, more rarely only one. It lies in the middle line dorsally, and is only rarely asymmetric (*Rattulidæ*, *Gastropus*). The cuticula is often elevated to a little hill, on the top of which a bunch of sensitive hairs, rarely only one single hair, is visible. In some cases, especially in loricate Rotifers, the hill is converted into a real antenna often situated immediately behind the wheel-organ, is drawn in together with the latter, and is the first which makes its appearance when the wheel-organ is again unfolded (*Brachionidæ*, *Anuræadæ*, *Salpinadæ*). In the *Bdelloida* it is segmented and provided with muscle threads, and may here as well as in some of the *Meliceridæ* reach a length of about one third of the body (*Cephaloziphon*); in *Eosiphora* HIRSCHFELDER (1910, p. 69) has interpreted the organ as a combination of a tactile and a static organ. The dorsal organ is very rarely absent (*Conochilus*). The posterior or ventral lateral organs hardly ever coalesce (perhaps in *Copeus caudatus*); they are almost always widely separated lying on the borders between the dorsal and ventral side and are provided either with a bunch of sensitive hairs or one single hair; they have not been ascertained in the *Bdelloida*. In the tubedwelling Rotifers they are often placed ventrally, situated upon long antenna-like organs, which are placed anteriorly so that their tips are the first part of the body which appears when the animals make their appearance outside the edge of the tube.

In the males these sensitive organs are constructed in accordance with those of the females; here however they are very difficult to detect; especially in many of the strongly reduced plancton Rotifers they are almost always unknown, and it is a question if they really exist here. In the *Asplanchna* they are identic in both sexes, and in many males, e. g. those of the genus *Synchaeta*, *Hydatina*, *Gastropus hyptopus* and others two nerves to the common dorsal organ are present. It is especially the

lateral organs, which are difficult to observe, and probably often overlooked. In the sessile families the *Flosculariidae* and *Meliceridae*, where the sense organs in the female sex show so many peculiar structures, they seem to be very much simplified in the male sex, and are never elongated into long antenna-like organs.

Most of the Rotifers possess sense organs for light in the female sex. They are lacking in *Pleurotrocha*, *Noteus*, *Callidina*, *Adineta*-species, and in the *Flosculariidae* and *Meliceridae*, when sessile; in the freeswimming stage they possess two eye spots. In accordance with DE BEAUCHAMP the position of the eye spots in Rotifera may be referred to the following scheme: an eye occipitale, often double and in contact with the brain, and the retrocerebral organ and two superior eyes on the disc or in the corona. As far as I know, the two sorts of light perceiving organs do not as a rule occur simultaneously. The common occurrence is the unpaired eye spot, below the brain; we have here a simple pigmented spot, a typical lens has not often been observed; it is however possible that the bacterioides in some species f. i. *N. pseudocerberus*, being situated in contact with the eye spot, and on its underside, may play a secondary rôle as light perceiving (DE BEAUCHAMP 1909, p. 174). Two eye spots exist in *Pterodinidae*, *Pedalionidae*, *Coluridae*, in some of the *Notommatidae* (*Diglena*) and a few *Asplanchna*-species. In the genus *Rotifer* they are placed upon the tip of the proboscis; as mentioned above they occur in the freeswimming stage of *Flosculariidae* and *Meliceridae* but very often disappear in the fixed stage. Two eye spots lateral also occur in *Eosphora*-species, but according to HIRSCHFELDER (1910, p. 86) these spots are not eye spots.

In the male sex it is interesting to see, that the number and position of the eye spots are almost always in accordance with those of the female. In those females which have one single eye spot, this is also found in the males; and when the females have two anterior eye spots, this is also the case with the males; in the *Eosphora* males we find three "eyes" as in the female; also the position of the eyes in the males of *Asplanchna*, is the same as in the females. This is also the case with *Triarthra*, but here as well as in the *Flosculariidae* it must be emphasised that the two eye spots in the male sex are placed upon a hill-like prolongation which, especially in *Triarthra*, has almost the character of a proboscis. In *Rhinops* the eye spots are situated upon the proboscis-like prolongation in both sexes. Especially in *Triarthra* and *Pedalion* typical lens organs have been observed. In some of the most reduced males I have been unable to find any trace of eye spots (*Polyarthra*, *Gastropus*, *Ploesoma*).

**Nephridia.** As well known, the nephridia of the Rotifera consist of two lateral canals, equipped with a number of vibratile tags and opening into the contractile bladder, which again debouches in the rectum. Commonly a transversal commissure between the two longitudinal canals is not observed; hitherto it has only been detected in *Stephanoceros*, *Atrochus*, *Conochiloides natans*, *Apsilus*, *Lascinularia* and *Hydatina*; it must however be remembered that just these Rotifers are the best studied of all. Everywhere where more elaborate investigations are carried on, it



has further been shown that the longitudinal canals really consist of two tubes, the secretory one (the Drüsengang MARTINI's) with relatively thick walls, often of glandular structure, and the excretory one (the "Flimmergang" MARTINI's) or capillary tube, which has very thin walls; it is this tube which carries the vibratile tags; the tube with the glandular structure commonly forms one or two windings or meanders in many loops and curves. It has much thicker walls and often contains oil globules. It is of great interest that HLAVA has found vibratile "Treibwimpern" (*Lacinularia*, *Megalotrocha*) in these tubes. The capillary tube debouches into the maintube by means of one or two transversal commissures. The structure of these two tubes, the excretory and secretory ones, their course and the manner in which they are connected with each other are subject to great variation in the different genera and species. The vibratile tags are connected with the tubes by means of short stalks, and project into the body cavity; their number is commonly from five to six on each side, but may in some *Asplanchna* species rise to about fifty. Most of the authors, especially those of recent years, are of opinion that the free broad end is closed; they are here provided with a protoplasmatic plug, which on the part turning towards the body cavity is as a rule provided with two flagellæ and upon the other part carries the vibratile flames, deriving from many cilia coalescent with each other: they are situated in the open space of the vibratile tags and are in constant motion. The canals debouch into the contractile vesicle, the walls of which are extremely thin and provided with very fine muscle threads; often, f. i. in *Asplanchna*, two large star-like cells with very long threads are observed; these cells have the function of contracting the bladder. This latter is commonly regarded as originating from the coalescence of the two excretory tubes. Only rarely is the vesicle absent (*Lacinularia*, *Tubicularia*). Here the two lateral canals coalesce into a common unpaired part; this part is in accordance with the contractile vesicle of Rotifers, but regular contractions have not been observed, the last part of the rectum functioning in this way (HLAVA). In the *Philodinidæ* part of the rectum is transformed and used as a contractile vesicle, being capable of rhythmical movements.

Commonly the whole organ is only regarded as an excretory organ; through the vibratile tags useless or destructive materia are carried out of the body. GOSSE however has supposed that the organ is respiratory, and as well known, EHRENBURG regarded it as the male sexual organ. In most of the Rotifers it may be observed that the bladder suddenly contracts regularly about four times a minute, in *Asplanchna priodonta* according to WILLEM (1910, p. 26) 4 times a minute, according to MASIUS (1890, p. 661) ten times; in *Adineta barbata* according to JANSEN (1893, p. 8) three to four times; then, in the intervals, it slowly fills again. The size of the bladder differs very much; WILLEM supposed that, in an *Asplanchna*, when distended, it is almost  $\frac{1}{5}$  of the body volume. In other words, during a time of only one to three hours, the organ was supposed to be able to collect and expel a volume of water, equivalent to the whole volume of the body. Apart from the difficulty of understanding that the body cavity should incessantly be run through by this enormous mass of

water, the question arises from where this enormous water current comes. Further, where are the forces which uninterruptedly drive the currents through the body cavity and where are the openings, through which the water finds its way into it? And lastly why should the body cavity be run through by such enormous water-masses? COHN, COSMOVICI and JANSEN have supposed that the bladder is in some way filled from the alimentary canal, and that its main task is to carry out of the body the water-masses which the animal has taken in through the mouth together with the food. "Sie hat, entgegen den früheren Ansichten, die Aufgabe, den durch die Räderorgane mit den Nahrungsteilchen in den Verdauungskanal hineingetrudelten Wasserstrom, der durch die starke Bewimperung des letzteren weiterbefördert wird, zu sammeln. Die Blase d. h. der dehnbare, dünnwandige Teil des Enddarmes wird durch das gesammelte Wasser aufgebläht und befördert dasselbe periodenweise durch Zusammenziehung nach aussen" (JANSON 1893, p. 8). JANSON further shows that the vesicle was contracted every 18 seconds, if the wheel-organ was fully expanded. If it was contracted, the contractions of the bladder were slower, first every twenty seconds, then every 25, 30, 40, 50 seconds and lastly they almost totally disappeared. As soon as the wheel-organ was again expanded, the contractions — about four in a minute — began again. According to JANSON this can only be interpreted to mean that the water is forced into the alimentary canal through the mouth, passes through the alimentary canal into the bladder, from which it is again poured out. Owing to the peculiar derivation and position of the contractile vesicle in the *Bdeloida*, the explanation of COSMOVICI and JANSON may be correct for these animals; but in the other divisions of the Rotifera it is difficult to understand that it can be quite exhaustive. The same ideas have, by the way, been set forth by WILLEM (1910, p. 26), who supposes that the watermasses especially pass through the thin walls of the oesophagus, and by GOSSE (1889, p. 138), who maintains that they "pass at the head."

In the male sex the excretory organ is only fully developed in the genus *Asplanchna*. Exactly as in the females we here find the two sorts of lateral canals, the secreting glandular tubes and the excreting capillary tubes which carry the vibratile tags. In the different species we find the same great difference with regard to the number of tags in the male sex as in the female sex; in *A. priodonta* in both sexes from 4 to 5 in *A. Sieboldi* about 40—50. The two lateral canals as in the female open in the contractile vesicle, and this again opens into the ductus seminalis. The vesicle is filled and contracted as far as I have been able to see quite in the same manner in the male as in the female. Fully extended it reaches an enormous size, in the male of *A. Sieboldi*, more than  $\frac{1}{5}$  of the body cavity. Apart from the *Asplanchnas* the contractile vesicle seems to be absent in almost all other Rotifer males. The two lateral canals which show a more simplified structure in the males than in the females, almost always seem to open with two small openings at the sides of the opening for the penis; but these openings are difficult to see. I for my own part have only been able to see them with certainty in *Salpina*,

*Floscularia* and *Hydatina*. Only rarely (*Asplanchna*) have two different kinds of lateral canals on each side been observed. As far as I have been able to observe, the vibratile tags are commonly implanted directly upon the glandular tubes, the capillary tubes being often absent; upon this point more thorough observations are however necessary. Even if the excretory organs are overlooked in many cases owing to the smallness of the organisms, there can be no doubt that they really do not exist in many of the smallest and most reduced males. This is the case with the males of *Conochilus*, *Notholca acuminata*, *Pompholyx sulcata*, *Polyarthra platyptera*, *Gastropus stylifer*, *Ploesoma Hudsoni*, *Rattulus*, *Triarthra*, *Pedalion*. If we remember that the life of these organisms most probably can be counted only in hours, this is quite intelligible.

The knowledge we have now gained with regard to the excretory organs in the males gives rise to the following remarks. There might be reason to suppose, that there could, in the male sex, be pointed out some connection between the occurrence of the alimentary canal and the developmental stage of the excretory organ; especially those who suppose that the water must come in through the alimentary canal, and the contractile bladder therefore in some way be filled from this organ, might expect that the contractile bladder would disappear where the alimentary canal is lacking, rudimentary, or functionless. That this is in some way really the case cannot be wholly denied; as mentioned above, it is a common rule that all males without alimentary canal are destitute of the contractile vesicle. On the other hand it must be remembered, that neither ROUSSELET nor I have been able to find this last named organ in *Rhinops vitrea*, one of the very few males which possess a fully developed alimentary canal and where therefore a bladder might be expected. Further, that the *Asplanchna* males which are entirely destitute of any alimentary canal, really possess a bladder, which is just as large as that of the female and functions perfectly. With regard to all those authors who suppose that the water currents in some way pass through the walls of the alimentary canal, it must now be emphasized that the contractile vesicle in the males of the *Asplanchna* is distended and emptied in quite the same manner as in the female sex, and this in spite of the total absence of an alimentary canal. As far as I can make out from our present standpoint of knowledge no other explanation is possible than that the water must pass into the body cavity from the whole surface of the animal. The driving forces are of course not the vibratile tags but only the difference between the density of the two fluids inside and outside the body wall. It is the main task of the vibratile tags to drive the water currents out of the body again. In the female sex they are provisionally stored up in the contractile vesicle from which they are at regular intervals forced out of the body, in the male sex this is not as a rule the case, and the water currents flow out uninterruptedly through the two openings at the side of the genital opening. This view is only of value as a working theory, but it might be tested by experimental investigation. If it is correct, our apprehension of the whole organ as only excretory must be somewhat altered; its main task being



not only to drive noxious material, deriving from the metabolism, out of the body, but also and mainly the volumina of water which by purely physical causes are forced into the body cavity. This supposition is by no means new; it has already been set forth by LEYDIG (1855, p. 82).

Remembering that in *A. priodonta* we only find about from 4 to 5 vibratile tags and in *A. Sieboldi* from 40 to 50 it is possible that a more thorough observation relating to the process of the filling of the bladder in these two species might perhaps elucidate something with regard to the function of the organ; lack of material has hindered me from making these investigations.

I cannot see better than, that there is still, in the anatomy of the Rotifera, an essential point relating to the excretory organ about which we lack almost all knowledge.

As we know that the *Asplanchna* males are most probably the males with the greatest longevity (about 4—7 days) whereas the strongly reduced males most probably only live for some hours and never 24 hours, it seems to me that the presence of the contractile vesicle is more dependent upon the longevity of the animal than upon the presence of a functioning alimentary canal.

Different authors have supposed that we should find special pores in the cuticula through which the water poured into the body cavity. LEYDIG (1855, p. 82) has supposed something in this direction, and EHRENBERG regarded the dorsal organ as a siphon.

In this connection we may call attention to the fact, set forth by KRÄTSCHMAR (1908) but hitherto never corroborated, that the peculiar sac which contains the great oil globule which is lying over the testis and which in some way "in enger Beziehung zu dem sehr schwierig zu beobachtenden Excretionsorgans steht", by means of a canal, ending in an always open porus, is in connection with the outer medium. "Es ist unschwer einzusehen, dass diese Einrichtungen darauf abzielen ständig das Excretionsorgan offen zu halten (1908, p. 9)." How great is the bearing of this observation, we do not really know. In this connection I take the liberty to call attention to the fact, that I have with absolute certainty seen in *Euchlanis* that the two lateral canals debouch in the sac above the testis and that I was unable to see the canals follow the ductus seminalis to the opening of the penis.

**Muscles. Females.** It is quite impossible in our present stage of knowledge to give a correct picture of the muscle system of the Rotifera. The muscles may be divided into transversal muscles, longitudinal muscles and muscles belonging to special organs, especially those of the mastax, the contractile vesicle and the stomach. The transversal muscles are particularly well-developed in the *Bdelloida*, where they often encircle the body at regular intervals to a number of twelve; they are here commonly interrupted ventrally. In the other orders and families their number is much smaller, commonly six or seven; extremely large only in *Atrochus*. In the loricate Rotifers they are not so well-developed; in most of the figures and descriptions they are wanting. The main task of the transversal muscle system is most

probably to press out the wheel-organ and foot by means of altering the pressure in the body cavity, when the organs have been drawn in by means of the longitudinal muscles.

The longitudinal muscles may commonly be divided into two groups, those of the anterior and those of the posterior part of the body; the former draw in the wheel-organ, the latter the foot; where the foot is rudimentary or absent, they are commonly greatly reduced. The two muscle groups overlap each other in the middle part of the body. The number, place and function of these longitudinal muscles are remarkably constant in the different genera and species, f. i. in the *Flosculariidae* and *Meliceridae*, where long longitudinal muscles pass through the whole body from the wheel-organ to the end of the foot. They have only been more thoroughly studied in very few species. The old division of ZELINKA in "Haut und Leibeshöhlemusculature" has now been discarded. It seems as if we find striated as well as smooth muscles; in some species special muscles, especially those of the wheel-organ, are conspicuously striated; MARTINI (1912, p. 614) maintains that, in *Hydatina*, excepting only two muscles, he only finds striated ones. Whether the muscle elements are to be regarded as muscle threads or muscle cells, cannot be stated with certainty. With regard to *Hydatina*, MARTINI has arrived at the main result that all the transversal muscles and all the more significant muscles are really muscle cells, muscle individuals with one nucleus only (exceptionally two).

**Muscles. Males.** The nature of the investigation prevents any elucidation of the histological structure of the muscles in the male sex; the division of the muscles in transversal muscles, longitudinal muscles, and those belonging to special organs, may also be maintained for the male sex; in most of the males we find from five to six transversal bands, most conspicuous in the more primitive families, in a few of them f. i. *Hydatina* even more. In some of the males, belonging to loricate families, the transversal bands are even more conspicuous in the males than in the females, (*Brachionidae*) but, especially in the males of the plancton Rotifers, not the slightest trace of a transversal muscle system has been detected (*Pedalion*, *Triarthra*, *Polyarthra*, *Pompholyx* a. o.). The longitudinal muscles are highly developed, especially the anterior group, in all the more primitive families, and where the foot is absent in the males, the posterior group is very much reduced.

Muscles belonging to special organs are almost absent; almost only the muscles of the penis belong to these and of the contractile vesicle of the *Asplanchna*; but in the most reduced males this seems almost to be lacking, the penis being protruded by means of alternation in pressure in the body cavity.

**Body cavity.** The body cavity of the Rotifera is filled with a fluid the nature of which is entirely unknown to us. In some Rotifers, f. i. the *Asplanchna*, it is extremely large, all the organs lying in their whole extension bathed in the fluid; in others it seems that the thickness of the hypodermis diminishes its space in a very high degree. As the hypodermis is thickest in the young, just born individuals, it will be understood that its size is augmented during growth. In the fluid are found

elements of different kinds; real blood cells have hitherto never been observed with certainty. In the body cavity of the females Spermatozoa which are often observed may be found swimming round in the fluid for a long time after pairing. In the plancton Rotifers it seems as if the body cavity often contains large quantities of oil globules; whether these are deposited in the hypodermic cells or are lying free in the body cavity it is difficult to say, but as I have seen them move when the animal is pressed, I have supposed that the last supposition in some cases may be correct; in the same species they may be developed to very different degrees, upon the greater or smaller quantities the hyalinity of the animal often depends. The quantity of oil is greatest in the newly hatched animals and may almost disappear when they have lived their longest time. It differs very much in the different families and species; in some of them it is very large, in others f. i. in most of the *Asplanchnade* it is almost entirely absent.

In the male sex, especially in the plancton Rotifers, it may be shown that the oil globules are mainly deposited on the dorsal side and that often a single, very large one, may be found almost in the middle of the animal, above or just before the testis. This f. i. is the case with the male of *Conochilus volvox*, *Floscularia*, *Notops brachionus*, *Gastropus stylifer*, *Ploesoma Hudsoni*. In others f. i. *Polyarthra platyptera* and *Pompholyx sulcata* large oil globules in different numbers are deposited above or before the testis. In others again especially the *Triarthra* males and those of *Pedalion* the globules are deposited quite irregularly throughout the whole body.

Where, in the plancton Rotifers, we have a single oil globule or a few dorsally situated fixed oil globules, I suppose that these globules have some bearing upon equilibration; it may be due to them that the males, during swimming, are always forced to turn the dorsal side upwards, preventing the rotating motion so characteristic of almost all females of Rotifers, but only rarely observed in the males which, contrary to the females, when swimming slowly, very often move in straight lines. A constant rotating motion of the males I have only observed in the males of *Asplanchna* that, as mentioned above, are also wholly destitute of oil globules.

Especially PLATE and ECKSTEIN, but also MASIVUS and with regard to *Apsilus* also GAST have stated that the body cavity contains threads and cells of connective tissue. It must however be pointed out, that with specific methods connective tissue has not hitherto been observed (*Hydatina* MARTINI 1912, p. 601). It may be possible that we really have to do with extremely fine muscle threads; as such I have regarded those threads which in the male sex are especially mentioned with regard to the *Asplanchna* species.

Now and then in some species we find, lying free in the body cavity, greater or smaller quantities of dark, often yellow coloured irregular masses; in the species they may in some specimens be comparatively large, in others they are but small or almost absent; their places differ from specimen to specimen, and it is most probable that they diminish with age; they are very conspicuous e. g. in the *Asplanchna* species. They have often been observed, and have always been regarded



as stored nutriment, yolkmasses, deriving from the egg. As it has been pointed out with regard to the *Asplanchna* species that the animals grow very considerably and that simultaneously herewith these masses diminish in size, it is most probable that this stored nutriment is really of significance in the short life time of these animals.

**Male organs:** The male organs in the Rotifera consist in 1) the testis, 2) the vas deferens or ductus seminalis, 3) the so-called prostata glands, 4) the penis.

The testis is a large, pearshaped or globular organ, lying in the middle of the body and often filling the greater part of the body cavity. Especially in the rudimentary males of the plancton Rotifers, f. i. *Polyarthra*, *Triarthra*, it is extremely large in comparison with the whole body. It is held in place by means of a broad, flattened band which reaches from the forepart of the testis to the wheel-organ, and as mentioned before commonly regarded as a rudiment of the alimentary canal. In some species, e. g. *Hydatina*, it is further fastened to the dorsal side by means of a special tissue, fastened to from three to five of the transversal muscle bands.

The development of the spermatozoa has been studied by WHITNEY (1917, p. 305 and 1918, p. 325), he states that the number in all the species investigated is remarkably small; the highest number of mature spermatozoa found in the testis being about 300 (*Asplanchna*). Earlier authors have often pointed out that the testis of the Rotifera contains two sorts of spermatozoa; the one sort has a well-developed head, and long undulating tail; these spermatozoa are very motile; the other sort are short, stiffened staffs, without head and immotile; the last named, almost always lie pressed together near the opening of the testis, almost parallel with each other; they were formerly (COHN) interpreted as a peculiar muscular structure of the testis; they are always much smaller in number than the motile ones. In two consecutive papers WHITNEY (1917, p. 305 and 1918, p. 325) has shown that the number of motile spermatozoa is exactly twice the number of immotile spermatozoa produced. Both sorts of spermatozoa possess heads, but the immotile spermatozoa are regarded as rudimentary and functionless. The functional spermatozoa, having fertilised a parthenogenetic male egg, always gives rise to a female individual. If the male egg had not been fertilised, a male would have been produced. Now as it has been ascertained, that in every male a certain percentage of the sperm-cells degenerate, and a certain percentage develop normally, thus giving a definite ratio of degenerate and normal sperm-cells, and as all fertilised eggs develop into female young, it seems safe to conclude that the degenerate sperm-cells are the male-determining ones, and that the normal sperm-cells are the female-determining ones (WHITNEY 1918, p. 333). It has often been supposed that the function of the staff-like rudimentary spermatozoa is to perforate the skin of the female during the pairing process.

The vas deferens, its length and its structure, is dependent upon the occurrence of a true penis.

In the most primitive forms the male sexual opening lies dorsally on the foot;

commonly on the last segment but one; the opening is almost always marked by means of a tuft of cilia. In the pairing moment the vas deferens in these forms is evaginated turned inside out, now showing a hyaline tube or cupshaped body, commonly at its base surrounded by a wreath of cilia, the same which originally presented itself as a tuft round the opening; a penis of this kind is found in all the *Notommatidae* hitherto observed, in *Hydatina*, in the *Flosculariidae* and in the *Meliceridae*, where it is placed on the very apex of the animal; it is of quite the same type in *Asplanchna*.

In many Rotifers we find a penis of a somewhat different kind. Round the opening for the penis on the dorsal side of the foot, the skin is folded, often somewhat resembling the so-called tail in the genus *Copeus*. By means of the transversal muscles and during the bending of the body, the fluid of the body cavity is pressed out into this part of the body; this is now altered into a stiff erectile organ, often much longer than the foot which only hangs down as a little ventral appendage.

A penis of this kind is most conspicuous in the *Brachionidae*, most probably also in *Euchlanidae* and *Salpinidae* and in *Gastropus hyptopus*. In these species the vas deferens is much longer than in the former group, and capable of great alterations with regard to length; as in *Hydatina* it is often transversally banded, most probably by very fine muscle threads.

In the *Anuraeadae* where both sexes lack a foot, the penis is always in an erect condition, hanging down from the posterior end; it cannot be drawn in. A penis of this peculiar type is best developed in *Anuraea hypelasma*.

In the most reduced males we find a penis of quite another type; here is really no penis at all. In the pairing moment the whole posterior part of the body is prolonged and often formed like a tube; this is most conspicuous in *Polyarthra*, *Pedalion* and *Triarthra*, where the posterior part of the body, when the animal is swimming, is rounded, but when used as penis, it is tapering. As mentioned above we commonly find a tuft of hairs at the opening, but in some species, f. i. of the genus *Anuraea*, we find two lateral hairs; this is also the case with *Triarthra* but here the opening is further supported by a chitinous frame.

The length of the vas deferens differs very much, and is in accordance with the structure of the penis; it is almost always coated with cilia; the walls are thin, transversally striped with muscle threads. In some cases f. i. *Brachionus* and *Diglena* the last part of vas deferens is transformed into a chitinous tube which, when used, is forced out of the genital opening. In *Brachionus* it ends in a cupshaped dilation; this is also the case with the penis in the genus *Rattulus*. In *Copeus labiatus* it is widened to a large sac.

At the sides of the vas deferens are two, rarely four glands, commonly designated as prostata glands.

They may be very large as in *Asplanchnopus* and *Hydatina* and where they are not indicated, it is most probably because they have been overlooked. In some species, f. i. *Polyarthra* and especially *G. hyptopus*, they have a peculiar lobate ap-

pearance. Above the testis, at the point where the testis tapers into the vas deferens, we very often, in the male sex, find one or two globular bodies, commonly hyaline sacs, filled either with one, two or many opaque corpuscles, often with sharp sides. They also occur now and then in the females, but much more rarely, their structure and size differ from specimen to specimen. They have been interpreted in very different ways by COHN and WEISSE as remnants of yolkmasses, deriving from the eggs, by LEYDIG as "Harnkonkremente" and the globular vesicle as rudiments of the rectum. Whether the last supposition is correct is perhaps doubtful, but as I have seen the lateral canals open into it, in *Euchlanis lyra*, I am inclined to think that LEYDIG's interpretation is really correct.

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## Chapter V.

### Remarks Relating to the Reduction of the Male Sex.

In the foregoing pages many examples have been given relating to the reduction of the male sex in the Rotifera. We have seen that the reduction may be carried so far that, as in *Polyarthra*, the male is really nothing but a sperm-sac, surrounded by a protoplasm, containing a number of oil globules and coated with a cuticula, anteriorly carrying a tuft of long cilia. If a freeswimming organism is really to play a rôle as a fertilising creature, it is obvious that a greater reduction, cannot take place. The question now is: What has caused this enormous reduction, a reduction so great that in the whole animal kingdom it is only very rarely met with, and most probably is really the most complete we, upon the whole, know.

As well known, the reduction of the male sex in the animal kingdom is by no means only restricted to the Rotifera. However, where it is not only limited to reduction with regard to size, it is almost always combined with parasitism. This is always the case where we have a reduction of such a radical nature that the males are really reduced only to sperm-sacs almost, with the necessary clasping organs for fastening or for locomotion. In many cases the males are parasitic upon or within the females. Strongly reduced males of this kind we find for instance in the *Cirripedia*, parasitic *Isopoda*, *Copepoda*, and in *Bonellia*. In the Rotifera however we have animals where parasitism of the males is an unknown phenomenon. Males and females live a freeswimming or freely creeping life, swimming side by side in the same water masses; at first sight it is wholly unintelligible what has caused this enormous reduction in the male sex.

We are here facing a problem which has not hitherto been solved, mainly because it has not been set up. Our hitherto very restricted knowledge of the male sex in the Rotifera is the main cause of this in itself very peculiar phenomenon. In the following pages an attempt is made to solve the question.



As mentioned often in this work, the most primitive types of the Rotifera like the Turbellaria live a creeping life either on the bottom or upon the vegetation. In all these primitive Rotifers, the eggs are not carried by the mother animal but laid upon a substratum. The difference in size between the three kinds of eggs, parthenogenetic female- and male-eggs, and fertilised resting eggs, is but small; the male eggs being most probably no more than one half shorter in diameter than the female eggs (See Tab. IX, fig. 2—6). The males are but slightly reduced; commonly the alimentary canal is rudimentary, but all the other organs are present, and even if the males are smaller than the females, they are of the same form and often resemble the females in a high degree.

The Rotifers which have diverged most from the primitive type, are the plancton Rotifers, those which have totally emancipated themselves from a substratum, living a pelagic life in the open water volumina, far away from a substratum of any kind. These Rotifers in the main lack all areas of support for depositing the eggs; commonly they carry the eggs themselves; a few of them either deposit them upon other plancton organisms or bring forth living young. Now it is just among these plancton Rotifers that the most reduced males occur.

If we study the size of the three kinds of eggs in one of the plancton Rotifers, it will be seen that there is here the greatest difference in size; especially the male eggs are extremely small; further that whereas a female producer carries only from two to four eggs, the male producer carries about 12—16 eggs; if they carry resting eggs their number is hardly ever more than one, rarely two. Moreover if we compare the amount of the total yolk-mass which is to be found in the total lot of male eggs with that which is found either in the female parthenogenetic eggs or in the resting egg, it will be seen that in all three cases it is almost of equal size, smallest perhaps in the resting egg (See Tab. XI, fig. 5—6). This in other words means that the total amount of yolk-mass which is at disposal in the given moment of egg-laying, is almost the same in all three cases. In one case the total amount is used for a single egg, in the other for two or four, but when the males are to be produced it is divided in no less than about sixteen different parts. The result is that the amount of nutriment with which each male egg is provided, is only about  $\frac{1}{3}$  to  $\frac{1}{4}$  of what a parthenogenetic female egg possesses. In accordance herewith the males must at birth be smaller than the females.

From these observations we are now able to understand the diminution in size of the plancton rotifers, but of the most interesting fact, that the males are not only reduced in size but also in their whole organisation, we have not hitherto got the slightest explanation. For this we must take quite different phenomena into consideration.

It is a well-known fact that the eggs of the plancton organisms are commonly very small; as often set forth this has most probably some connection with the fact that the plancton organisms are mainly forced to carry the eggs and that therefore the quantity of yolk-mass with which the eggs may be provided can only be relatively

small, in accordance with the force of the mother animal. This fact is again connected with the phenomenon that the individuals, on coming out of the eggs, are very much smaller than the parents and are in a stage of development far from that in which the parents were. It is only through a series of larva stages that these young ones, by means of food reception, slowly grow up to the mature stages. Often they take about a year before these are reached (f. i. many Copepoda which are hatched in the autumn months). In some plancton organisms we find care for the offspring, the young ones living for a long time in the brood-room of the mother animal.

Now as far as I know, among all Metazoa, the Rotifera are the only plancton organisms which neither possess any metamorphosis nor show any care for the young.

Deriving from fresh water turbellaria where a metamorphosis does not exist, they were originally found to live in a medium where larva stages are either totally suppressed or at any rate only play a very inconspicuous rôle. As well known, with regard to the pelagic region of the sea and the freshwaters, there is the great difference that, whereas the firstnamed teems with larva stages, especially belonging to benthonic animals, these are almost quite absent in the pelagic region of the freshwaters, where the Benthos hardly ever produces pelagic larva stages and where, of the plancton organisms, these as a rule occur only in the Copepoda. — This lack of metamorphosis in the Rotifera must enter into our calculations, if we will try to understand the main causes of the reduction of the male sex.

In those cases where we possess a more thorough knowledge with regard to the rate of development of the male eggs in the Rotifera, we know that this may be finished in the course of only 24—36 hours. Only one or two days after the egg has left the mother animal and has been attached to the posterior part of its body, the cleavage process is finished, the egg shell bursts, and the male is a free-swimming organism. We are further able to substantiate that the spermatozoa in the testis are in full motion for several hours before the eggs are hatched. Finally if we have some *Polyarthra* or *Anuræa* females (male producers) in a drop, we will see that in the very same hour in which they are hatched the pairing will take place. The males so to speak rush from the eggshell directly upon the females, ready to pair in the moment of birth.

From the two now established facts, that the total amount of yolkmass of the female is to be distributed over many individuals, and that this is just the case with a group of animals where metamorphosis does not occur, I find some clues to the explanation of the reduction of the male sex in the Rotifera. It is in the first place dependent on the fact that the amount of yolk mass, which the egg is provided with in the plancton Rotifers as well as in almost all other plancton organisms, is extremely small. This caused the diminution in size of the male sex. The great reduction of the common organisation is based upon the second phenomenon, that the Rotifera belong to those organisms which are destitute of a metamorphosis, larva stages like those of so many freshwater organisms being wholly unknown. After birth the males get no time to build up their bodies by the reception of food beyond

the stage in which they are born. During the embryonic development stress is only laid upon the formation of the male organs, the material given to the egg not allowing of a more elaborate development of the organism.

We have now I presume got some material to elucidate some of the facts which produced the strongly marked reduction of the male sex, most pronounced in the plancton Rotifers. But of the deeper lying causes why the reduction of the male sex especially in the plancton Rotifers was really a *conditio sine qua non* for these organisms from the moment, when they were to pass from creeping bottom organisms into freeswimming organisms, take possession of the open waters, and emancipate themselves from any substratum therein, we have hitherto had no explanation at all. — The strongly marked reduction of the male sex is really of the greatest advantage for the species. This will be understood from the following considerations and observations.

When the quantity of yolk mass which is at the disposal of the female, and which is to be used for the preparation of the males, is distributed over as large a number of individuals as possible, it is obvious that it is possible for the males, in comparison with the females, to come in an enormous majority. Now it is a well-known fact that the male producing females in a lake almost all come up simultaneously, viz. in the last part of a maximum, further, that the enormous amount of male eggs all develop almost simultaneously, viz. in the course of about eight days. This again in other words means that the total amount of material of impregnation in these very eight days is distributed over an enormous quantity of individuals. The possibility of pairing between the two sexes is augmented in a very high degree, that phenomenon upon which depends in the first line the formation of resting eggs, which again in many cases is a *conditio sine qua non* for keeping the locality for the species.

As the smallest males of the plancton Rotifers cannot be caught with our plancton nets, we have not the slightest idea of the incredible numbers of males developed in the water layers, during the sexual period of a species. But if in this period we catch large amounts of plancton, as far as possible strain away the larger plancton organisms f. i. Daphnids and Copepoda, and let the rest stand over for a night in great jars, the next morning at the surface rim, turning towards the light source, we shall find a milky border, consisting almost entirely of males. This phenomenon I have observed often enough with regard to *Polyarthra platyptera*, *Pompholyx sulcata* the *Anuræa* and *Brachionus* species. — But it can only be observed in the short sexual periods, never outside these; the occurrence of the sexual period in the plancton Rotifers may be compared with phenomena that are well known in the vegetable kingdom f. i. the period, when the conifera throw their pollen, and the flowering season of the rye.

In all cases it is the material for impregnation which, in a few days and hours, fills the surrounding medium; the result of the process is in the one case the seed, in the other, the resting-egg. In the autumn the resting eggs come to the surface;



on putting a milky white glass plate immediately under the surface of a calm lake, it will be seen that its surface film carries an enormous amount of resting eggs, these are later on, when swept away by the autumn storms, deposited as dark lines near by or upon its shores.

It is this spreading of the impregnating material to innumerable individuals which was in my opinion a *conditio sine qua non* for the remodelling of an originally creeping organism into a freeswimming one, and which could only take place at the sacrifice of the size and stage of development of the males.

Thus I suppose we have some leading points that will enable us to understand partly the underlying principles which made the reduction of the male sex desirable for the species, and partly why the males if the species was to try to fulfill the claims which were laid upon it in this respect must necessarily, owing to want of food, be reduced in size.

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## EXPLANATION OF PLATES

All plates reduced with one third.

### Tab. I.

Fig. 1. Notommata najas .....	seen dorsally.	Obj. 4. Oc. 6
- 2. — .....	seen ventrally.	Obj. 4. Oc. 6
- 3. Notommata aurita.....	seen ventrally.	Obj. hom. Im. Oc. 6
- 4. Proales parasita .....	seen dorsally.	Obj. hom. Im. Oc. 6
- 5. — .....	seen ventrally.	Obj. hom. Im. Oc. 6
- 6. — .....	Wheel-organ seen in front.	Obj. hom. Im. Oc. 6
- 7. Diglena grandis .....	seen laterally.	Obj. hom. Im. Oc. 6
- 8. — catellina.....		Obj. hom. Im. Oc. 6
- 9. — giraffa.....		Obj. hom. Im. Oc. 6

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Fig. 1. Copeus labiatus .....	seen dorsally.	Obj. hom. Im. Oc. 6
- 2. — pachyurus .....	seen dorsally.	Obj. hom. Im. Oc. 6

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- 2. — tremula .....	seen laterally.	Obj. hom. Im. Oc. 6
- 3. Polyarthra platyptera .....	seen dorsally	Obj. hom. Im. Orthoscop Oc.
- 4. — .....	seen ventrally.	Obj. hom. Im. Orthoscop Oc.
- 5. Rattulus stylatus .....	seen laterally.	Obj. hom. Im. Oc. 6
- 6. — pusillus .....	seen laterally.	Obj. hom. Im. Oc. 6
- 7. — — lorica contracted .....	seen laterally.	Obj. 4. Oc. 4
- 8. — cylindricus .....	seen ventrally.	Obj. hom. Im. Oc. 6

### Tab. IV.

Fig. 1. Euchlanis dilatata.....	seen ventrally.	Obj. hom. Im. Oc. 6
- 2. — lyra.....	seen dorsally.	Obj. hom. Im. Oc. 6
- 3. — triquetra .....	seen laterally.	Obj. 4. Oc. 6

### Tab. V.

Fig. 1. Salpina mucronata .....	seen laterally.	Obj. hom. Im. Oc. 6
- 2. — spinigera .....	seen laterally.	Obj. hom. Im. Oc. 6

Fig. 3. <i>Metopidia lepadella</i> .....	seen ventrally.	Obj. hom. Im. Orthosc. Oc.
- 4. <i>Euchlanis lyra</i> .....	seen ventrally.	Obj. hom. Im. Oc. 6
- 5. — <i>dilatata</i> .....	seen dorsally.	Obj. 4. Oc. 4
- 6. <i>Asplanchna priodonta</i> . Fig. 6a the newly born young one with great amount of store nutriment. Fig. 6b the same animal five days later; larger, and with reduced store nutriment .....		Obj. 4. Oc. 6

## Tab. VI.

Fig. 1. <i>Microcodides robustus</i> .....	seen dorsally.	Obj. 4. Oc. 6
- 2. — .....	seen laterally.	Obj. 4. Oc. 6
- 3. <i>Gastropus hyptopus</i> .....	seen laterally.	Obj. hom. Im. Oc. 6
- 4. — .....	seen dorsally.	Obj. 4. Oc. 6
- 5. — Penis extruded .....		Obj. hom. Im. Oc. 6
- 6. <i>Asplanchna priodonta</i> . Penis extruded; phase 1 .....		Obj. 4. Oc. 6
- 7. — — phase 2 .....		Obj. 4. Oc. 6

## Tab. VII.

Fig. 1. <i>Asplanchna priodonta</i> .....	seen dorsally.	Obj. Waterim. Oc. 4
- 2. — <i>Brightwelli</i> .....	seen laterally.	Obj. Waterim. Oc. 6
- 3. — <i>Sieboldi</i> .....	seen laterally.	Obj. Waterim. Oc. 4
- 4. — <i>amphora</i> .....	seen laterally.	Obj. Waterim. Oc. 6

## Tab. VIII.

Fig. 1. <i>Hydatina senta</i> .....	seen dorsally.	Obj. hom. Im. Oc. 6
- 2. — .....	seen ventrally.	Obj. hom. Im. Oc. 6

## Tab. IX.

Fig. 1. <i>Hydatina senta</i> .....	seen laterally.	Obj. hom. Im. Oc. 6
- 2. — female egg .....		Obj. 16. Oc. 4
- 3. — male egg .....		Obj. 16. Oc. 4
- 4. — resting egg .....		Obj. 16. Oc. 4
- 5. — A piece of algæ carpet with the three sorts of eggs and some males; seen from below .....		Obj. 4. Oc. 2
- 6. — the same .....	seen laterally.	Obj. 4. Oc. 2
- 7. <i>Proales parasita</i> Male .....		
- 8—15 demonstrates the variation in form of the female, after having pierced an <i>Uroglena</i> colony; 8 and 9 freeswimming stages...		Obj. 4. Oc. 4

## Tab. X.

Fig. 1. <i>Rhinops vitrea</i> .....	seen ventrally.	Obj. hom. Im. Oc. 6
- 2. — .....	seen laterally.	Obj. hom. Im. Oc. 6
- 3. <i>Hydatina senta</i> . Penis extruded phase 1 .....		Obj. 4. Oc. 6
- 4. — — phase 2 .....		Obj. 4. Oc. 6
- 5. <i>Notops brachionus</i> .....	seen dorsally.	Obj. 16. Oc. 6
- 6. — .....	seen laterally.	Obj. 16. Oc. 6

## Tab. XI.

Fig. 1. <i>Brachionus pala</i> .....	seen dorsally.	Obj. hom. Im. Oc. 6
- 2. — .....	seen laterally.	Obj. hom. Im. Oc. 6

Fig. 3.	<i>Brachionus pala</i> , lorica	seen dorsally.	Obj. 4. Oc. 6
- 4.	— <i>urceolaris</i>	seen ventrally.	Obj. hom. Im. Oc. 6
- 5.	<i>Pedalion mirum</i> female eggs		Obj. 4. Oc. 6
- 6.	— male eggs		Obj. 4. Oc. 6
- 7.	<i>Floscularia ornata</i> female egg		Obj. 4. Oc. 6
- 8.	— male egg		Obj. 4. Oc. 6
- 9.	— resting egg		Obj. 4. Oc. 6
- 10.	— young one, leaving the egg		Obj. 4. Oc. 6

## Tab. XII.

Fig. 1.	<i>Brachionus angularis</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 2.	—	seen laterally.	Obj. hom. Im. Oc. 6
- 3.	<i>Schizocerca diversicornis</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 4.	—	seen laterally.	Obj. hom. Im. Oc. 6

## Tab. XIII.

Fig. 1.	<i>Anuræa aculeata</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 2.	—	seen laterally.	Obj. hom. Im. Oc. 6
- 3.	<i>Anuræa cochlearis</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 4.	— lorica	seen dorsally.	Obj. hom. Im. Oc. 6
- 5.	<i>Anuræopsis hypelasma</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 6.	—	seen ventrally.	Obj. hom. Im. Oc. 6
- 7.	<i>Notholca acuminata</i>	seen laterally.	Obj. hom. Im. Oc. 6

## Tab. XIV.

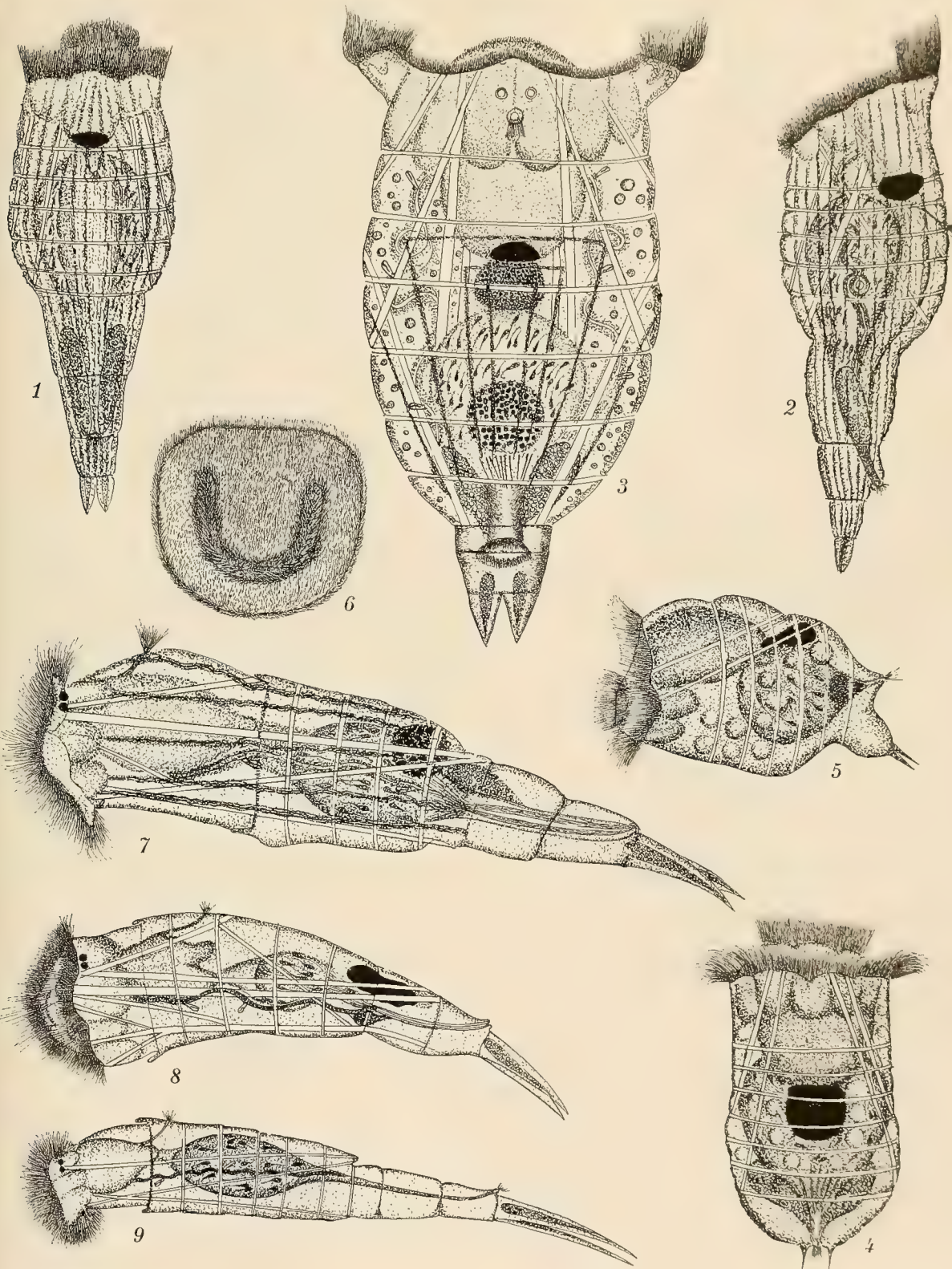
Fig. 1.	<i>Pompholyx sulcata</i>	seen dorsally.	Obj. hom. Im. Orthoscop Oc.
- 2.	<i>Gastropus stylifer</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 3.	—	seen laterally.	Obj. hom. Im. Oc. 6
- 4.	<i>Ascomorpha agilis</i>	seen laterally.	Obj. 4. Oc. 6
- 5.	<i>Ploesoma hudsoni</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 6.	—	seen ventrally.	Obj. hom. Im. Oc. 6
- 7.	<i>Pedalion mirum</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 8.	—	seen laterally.	Obj. hom. Im. Oc. 6

## Tab. XV.

Fig. 1.	<i>Triarthra longiseta</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 2.	— <i>mystacina</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 3.	— <i>breviseta</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 4.	<i>Conochilus volvox</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 5.	—	seen laterally.	Obj. hom. Im. Oc. 6
- 6.	<i>Floscularia ornata</i>	seen dorsally.	Obj. hom. Im. Oc. 6
- 7.	—	seen laterally.	Obj. hom. Im. Oc. 6

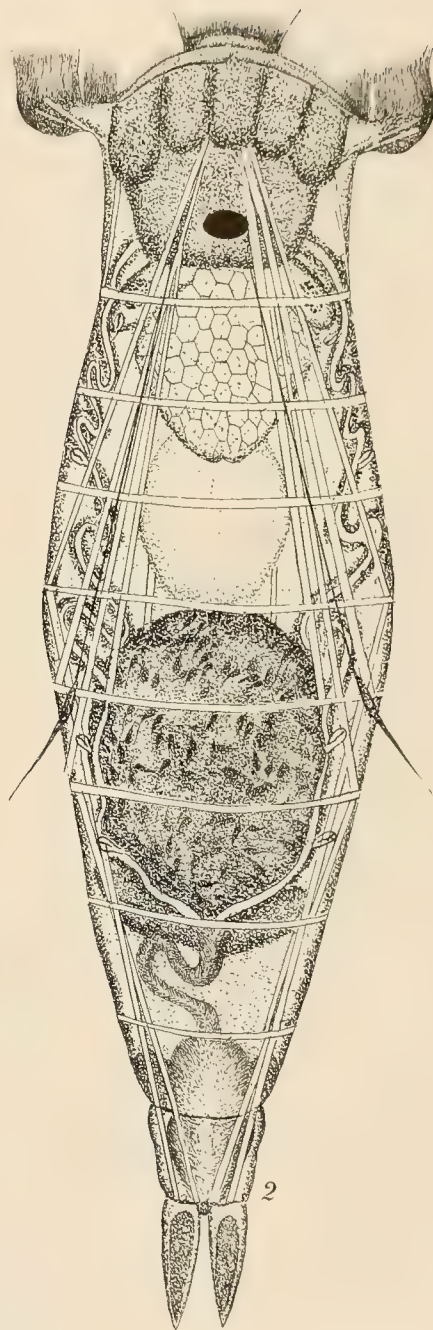
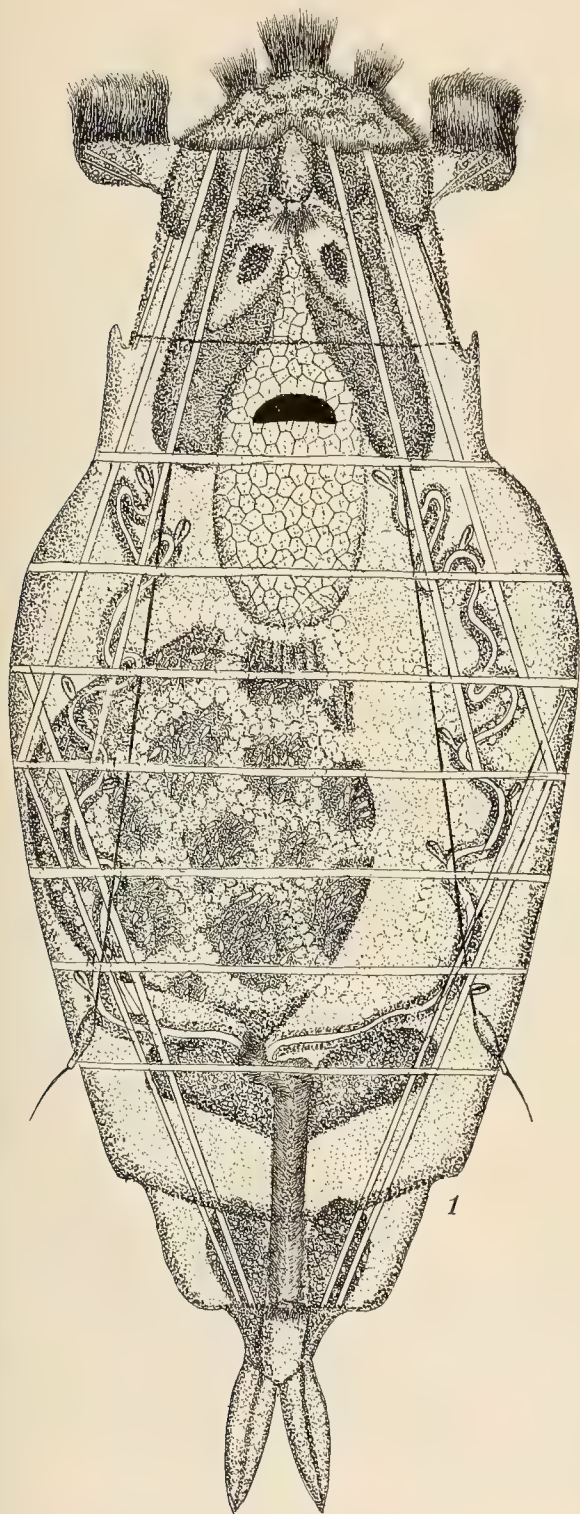






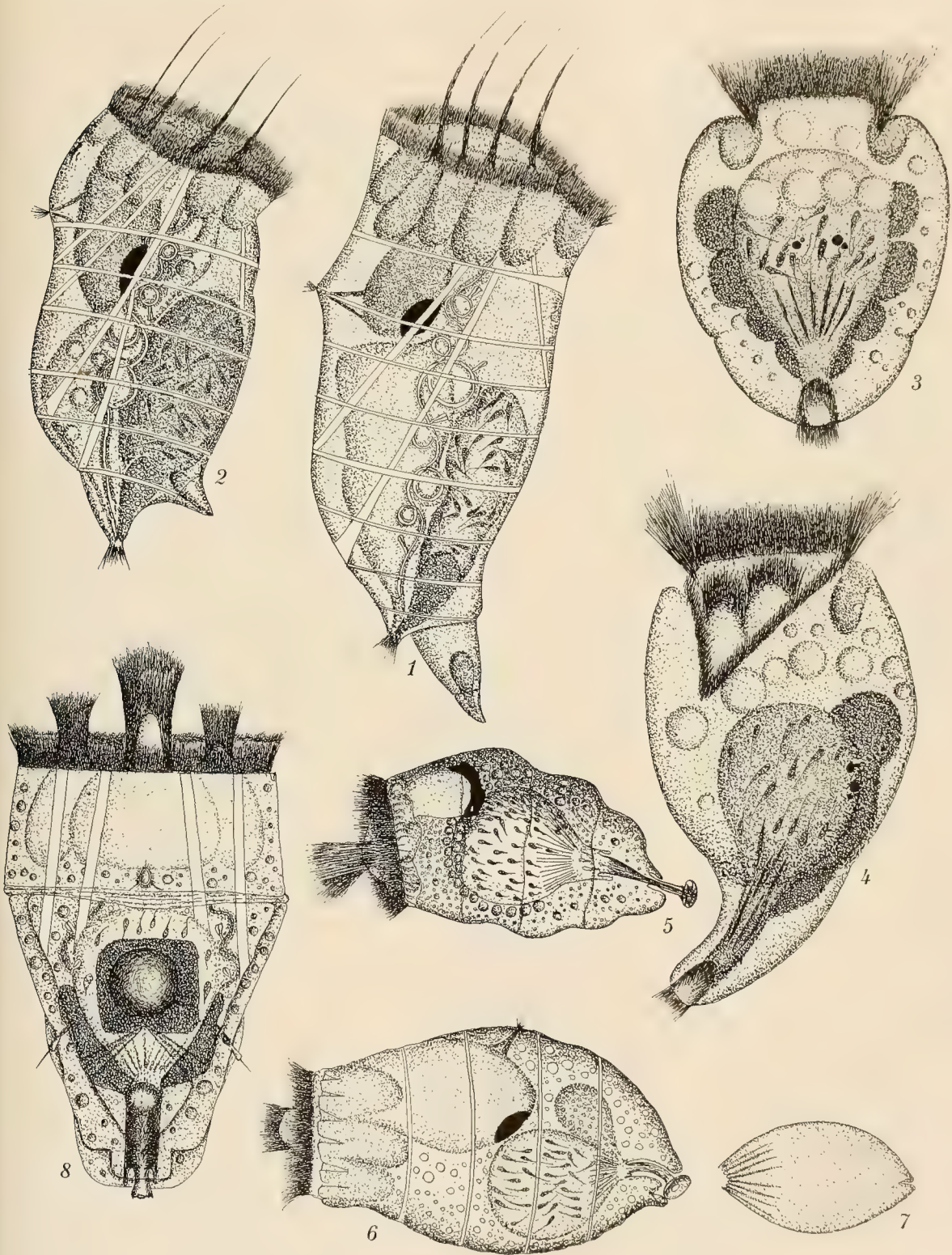






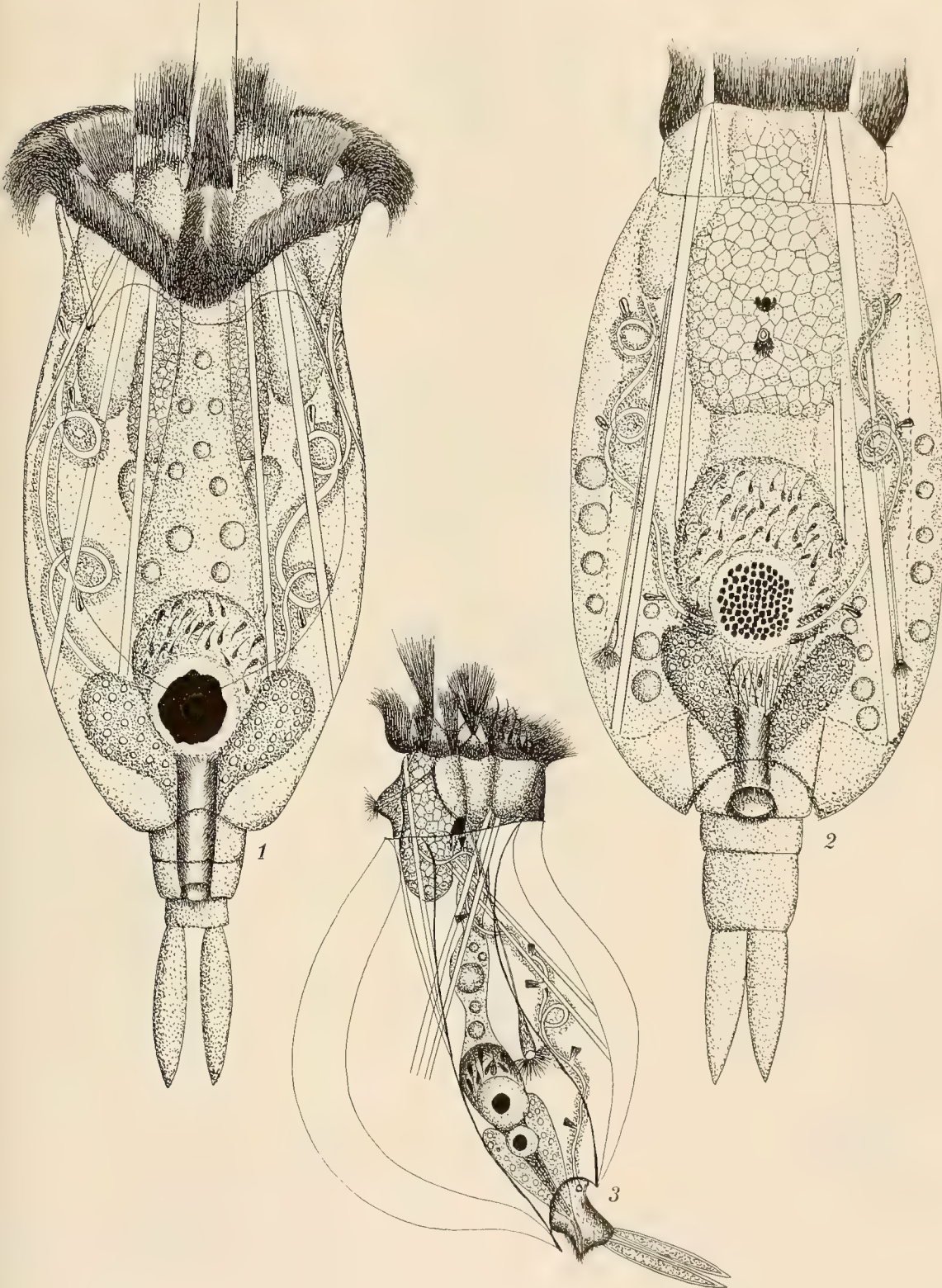










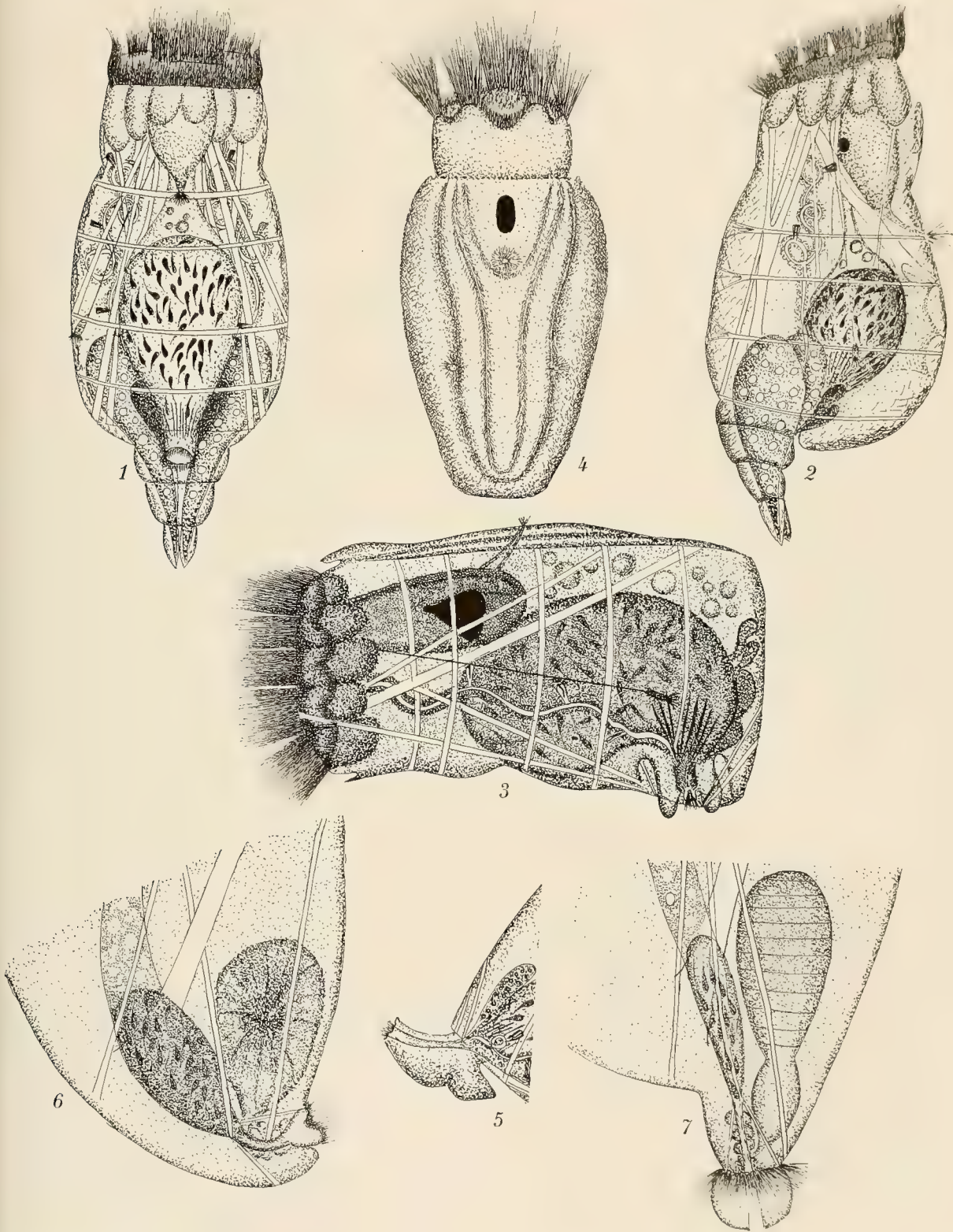






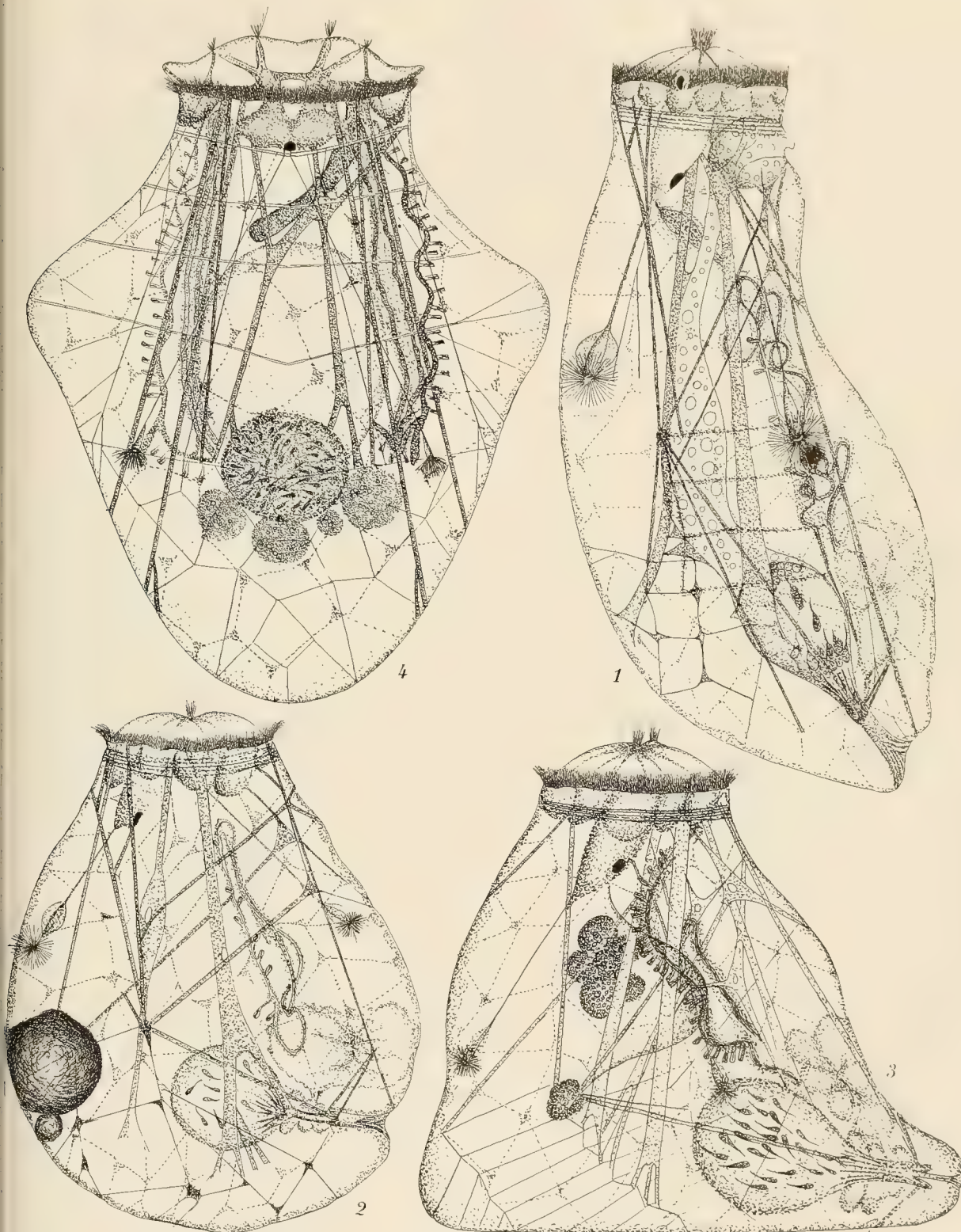






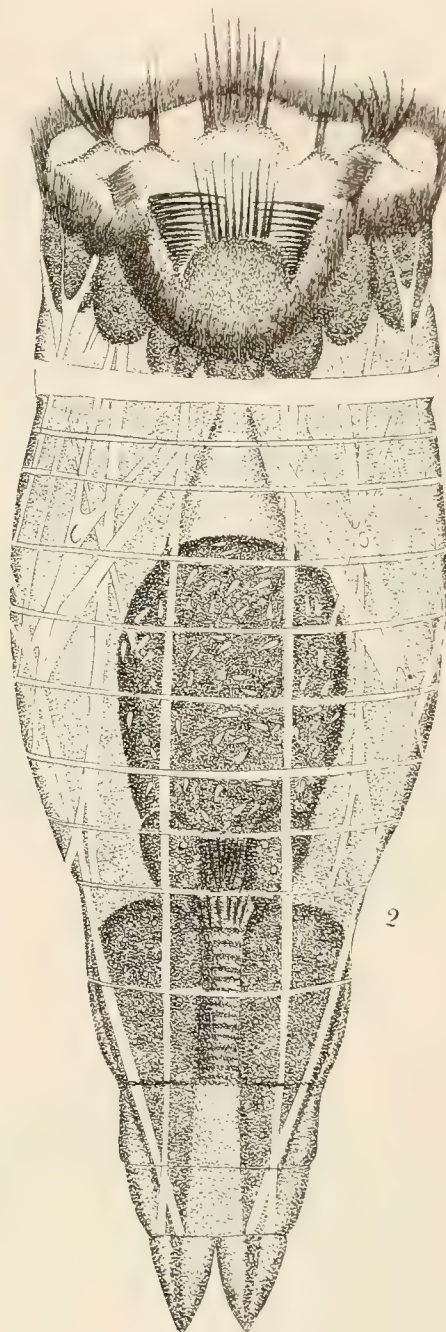
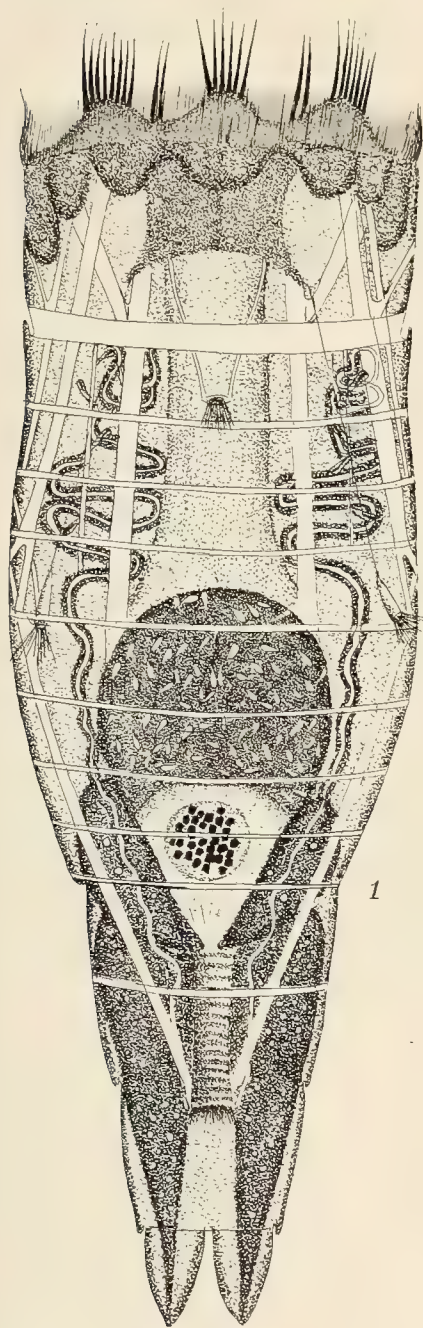




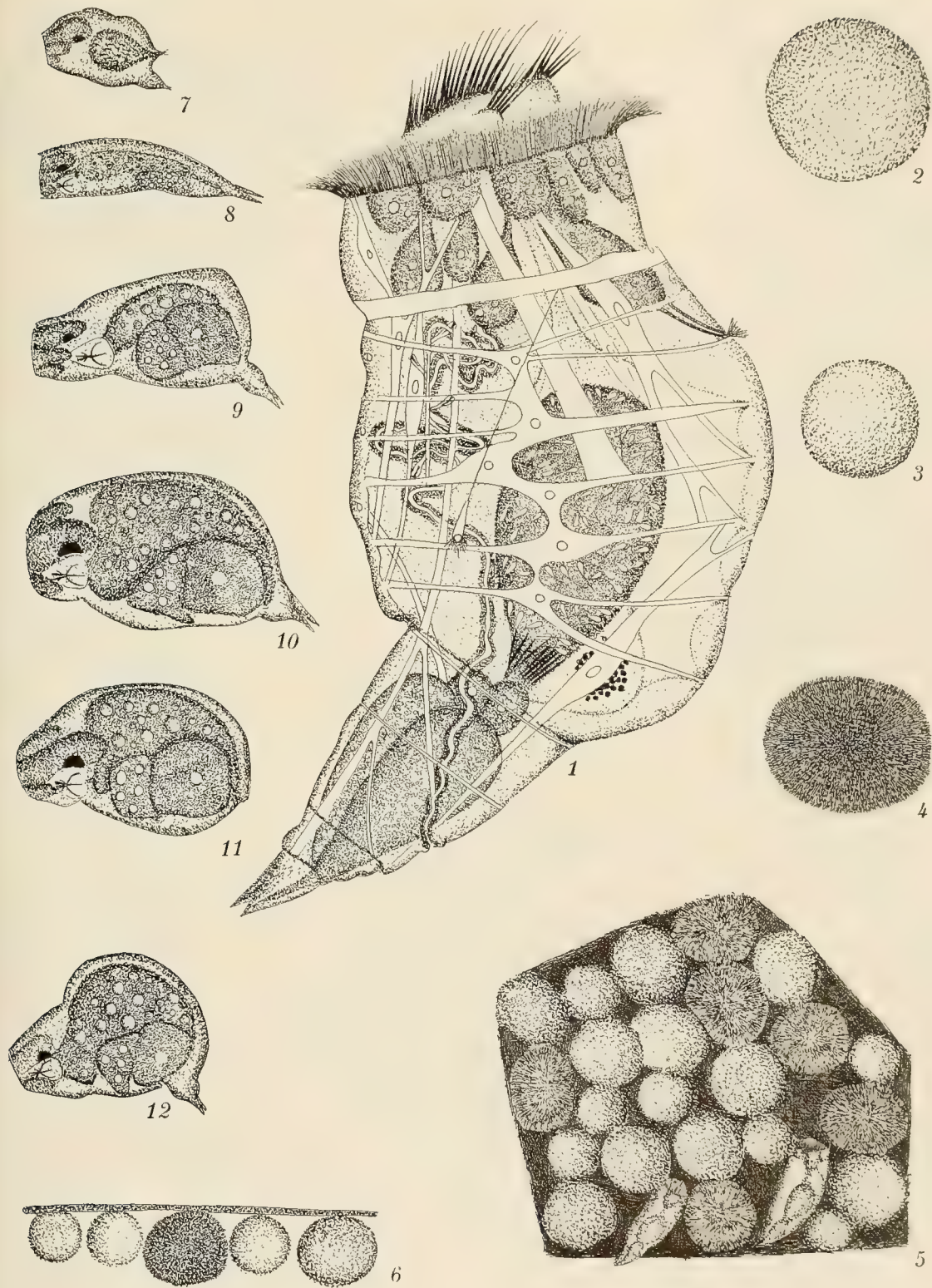






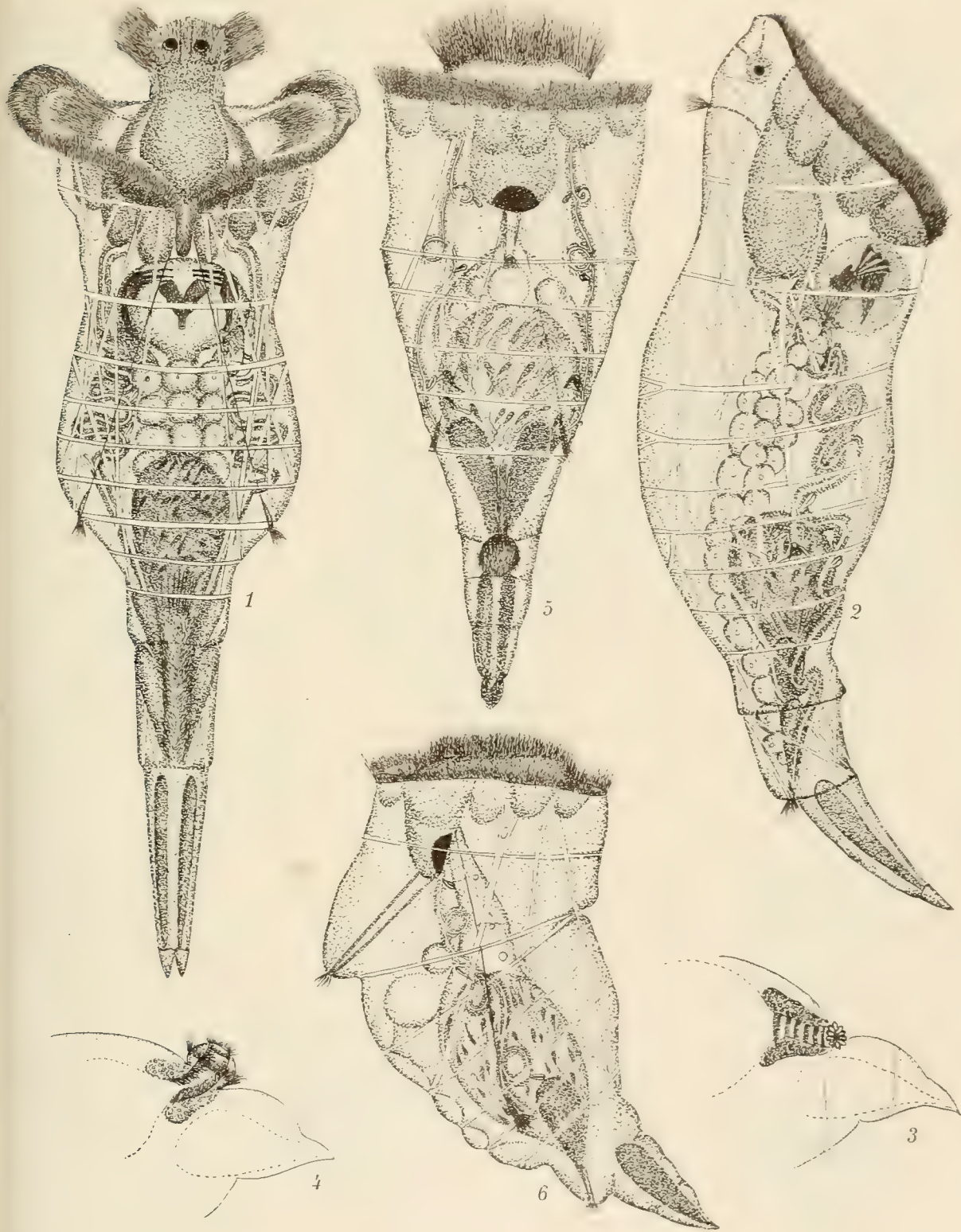






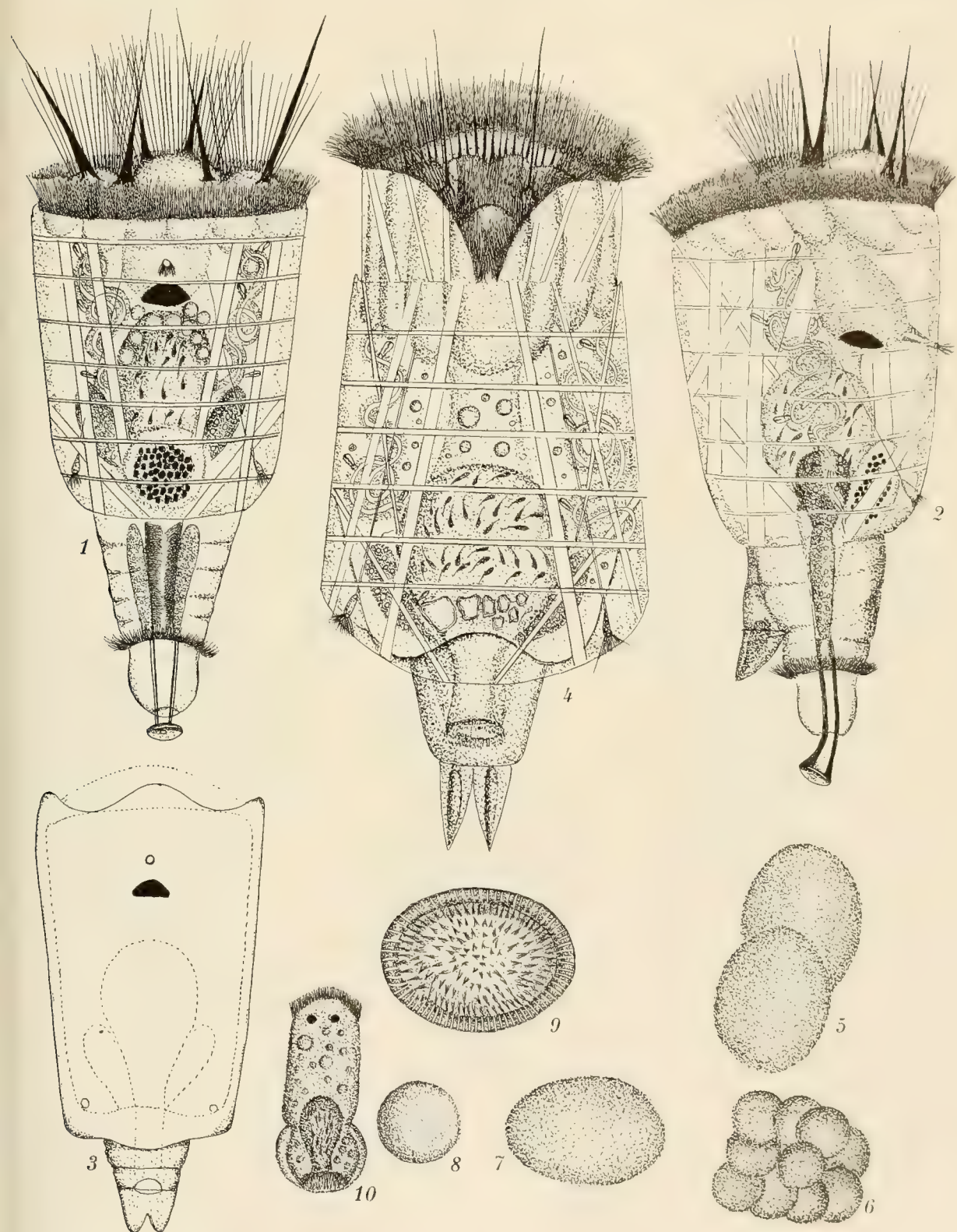




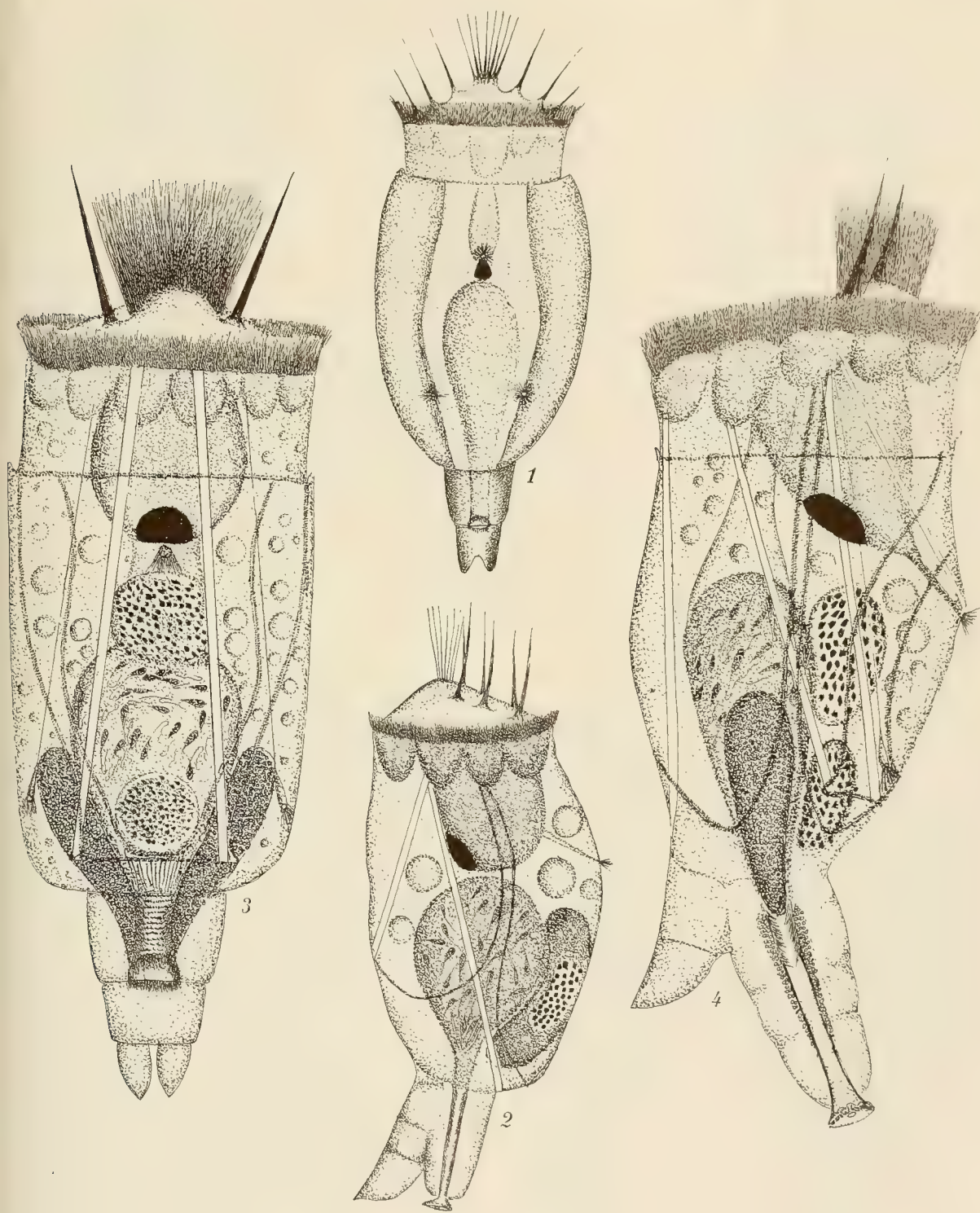






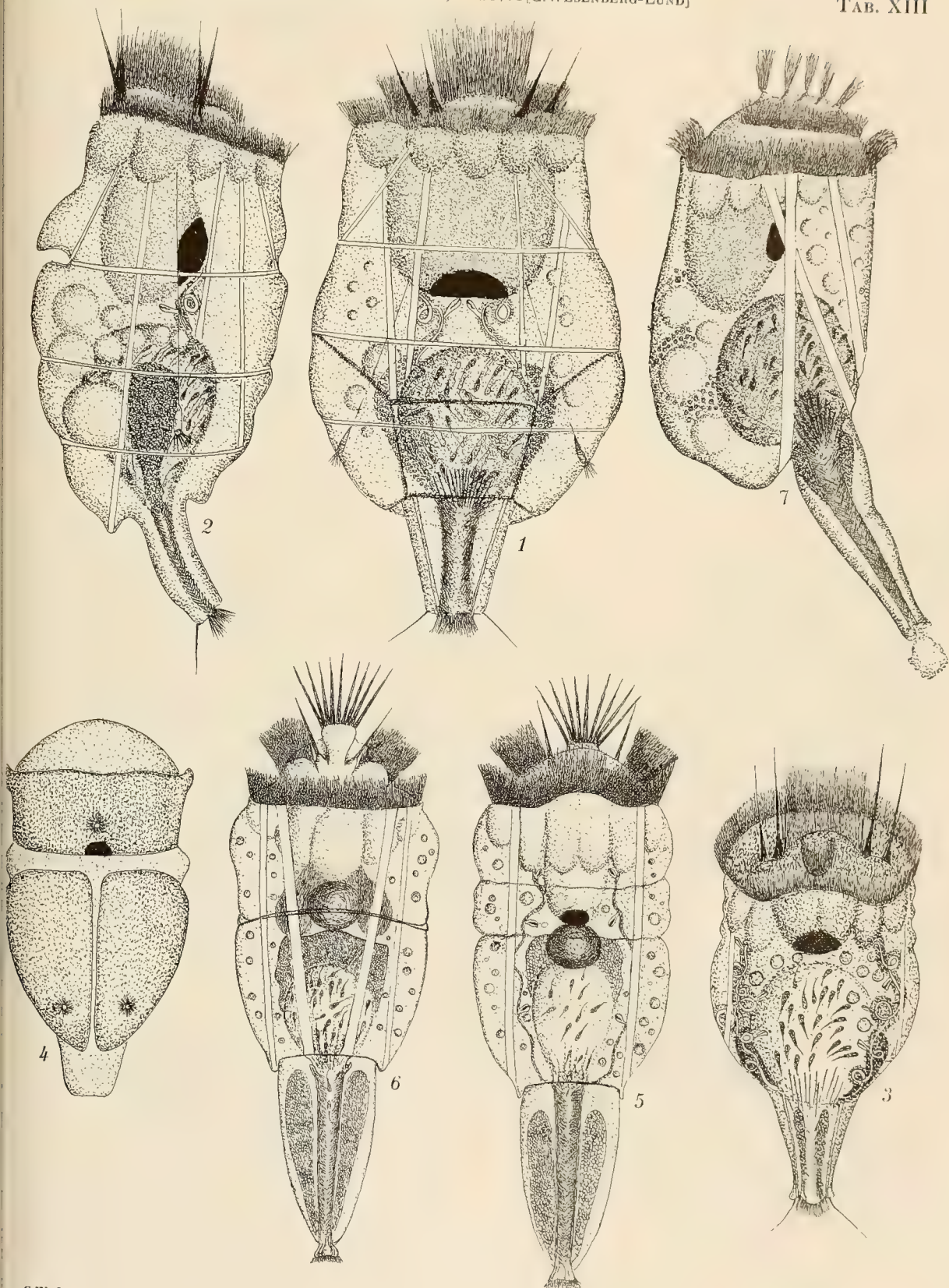






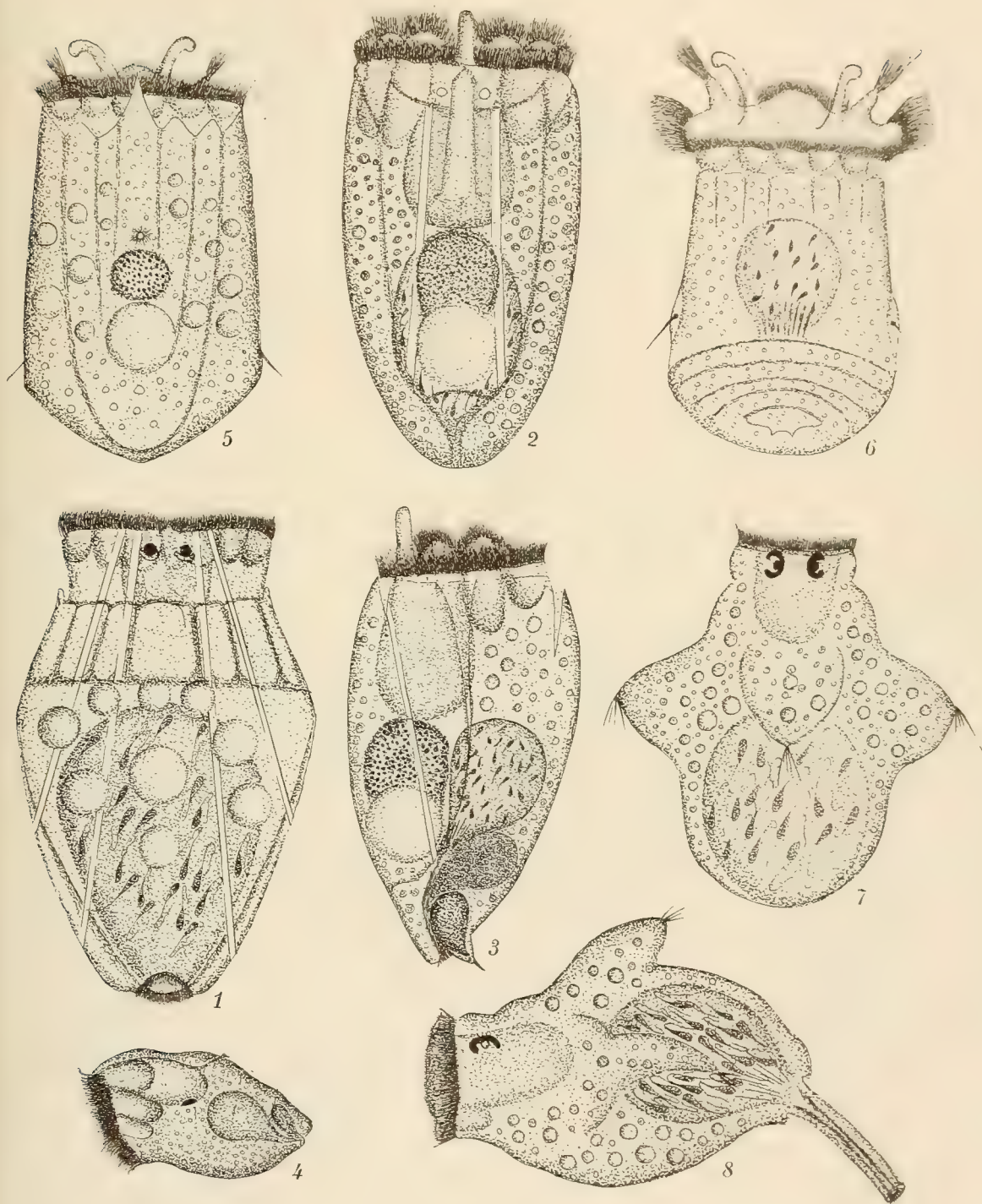




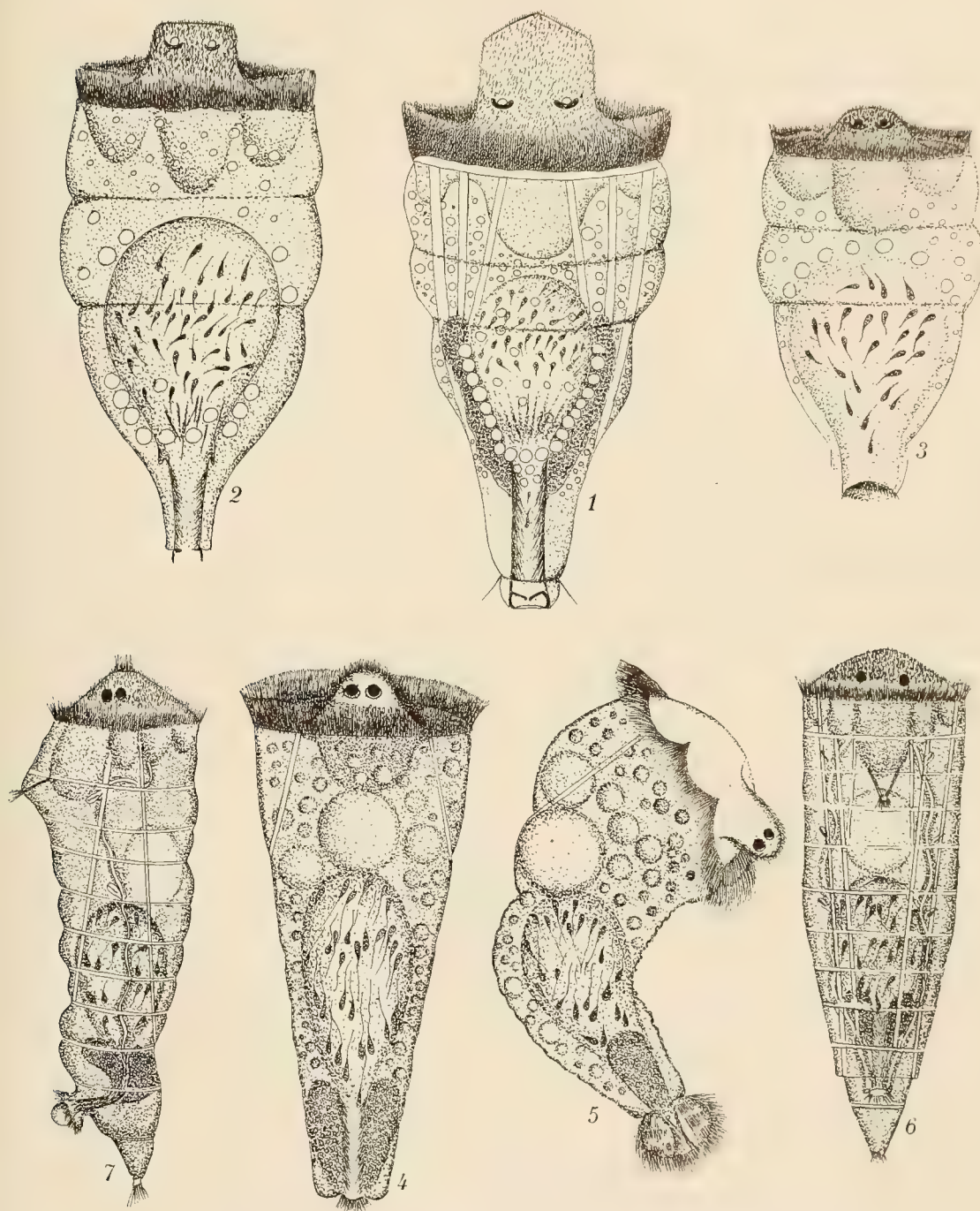
















# EFFECTIVE WAVELENGTHS OF STARS IN THE PLEIADES FROM PLATES TAKEN AT MOUNT WILSON

BY

EJNAR HERTZSPRUNG

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WITH 4 FIGURES AND 1 MAP

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BIANCO LUNOS BOGTRYKKERI

1923





## 1. Introduction, Instrumental Constants.

The present investigation has mainly been undertaken from the following point of view.

The Pleiades have always been the object of special attention. As a consequence of this a number of old photographs with long exposures of this group is available. These plates have partly been taken with lenses of sufficient focal length to enable a good determination of relative proper motions of faint stars by comparison with more recent plates. Owing to the considerable number of such old photographs the attainable accuracy will perhaps be greater for this group than for any other region of the sky.

It is to be regretted that the determination of absolute proper motions of the fainter stars by connection with the brighter ones of known proper motions is made difficult by the unknown magnitude equation occurring in photographic work of this kind. But just in the group of the Pleiades we may hope through accurate measures to find out, which stars, also among the fainter ones, have a proper motion common to the system and which have not. Of course, a certain arbitrariness will always remain in the separation of these two groups. Determinations of radial velocity would help to distinguish physical members from stars only optically projected on the part of the sky considered. We should then be able to use the stars of supposed common proper motion but of different brightness for the elimination of the magnitude equation.

Once the separation between physical and only optical members of the group is made, the determination of colour equivalents of the same stars will give us: Firstly, the relation between absolute magnitude and colour of the members of this interesting system, and secondly, the relation between apparent magnitude, colour and proper motion of faint stars in a special well observed region of the sky. Therefore I included the Pleiades in my programme for the determination of effective wavelengths with the 60 inch reflector of Mount Wilson. I had the prospect, in this way to get colour-equivalents of as faint stars as occur on the old photographs fit for the determination of relative proper motions.

The conspicuous group of the Pleiades has a diameter of about  $2^\circ$ , while the 60 inch reflector using the full aperture has a field of only about  $20'$  diameter fit

for the determination of effective wavelengths. I have therefore diminished the number of plates necessary to cover the whole group by diaphragming the reflector down to an aperture of 40 inches or 1 meter. In this way the diameter of the efficient field is doubled to about  $40'$ , while on the other hand for stars near the axis 1 magnitude is lost. Still it could be foreseen, that in half an hour of exposure time stars of the 14<sup>th</sup> magnitude would be reached. — The 68 plates of the programme have all been taken.

The place of the reflector is  $7^h 52^m$  W. of Grw.,  $34^\circ 13'$  north latitude and 1730 meter above sea level. Hence the thickness of the atmosphere is  $\cdot 81$  of that

at sea level. The focal length of the reflector is 7606 mm, hence 1 mm on the plate is equal to  $27''\cdot 12$ .

The grating used consisted of black overspun, stretched rubber wires of a diameter  $d = 2\cdot 745$  mm separated by intervals  $l = 3\cdot 255$  mm. The spectra of uneven order are thus practically (if  $d = l$  exactly) at their maximum intensity. The constant of the grating,  $d + l$ , was exactly 6 mm.

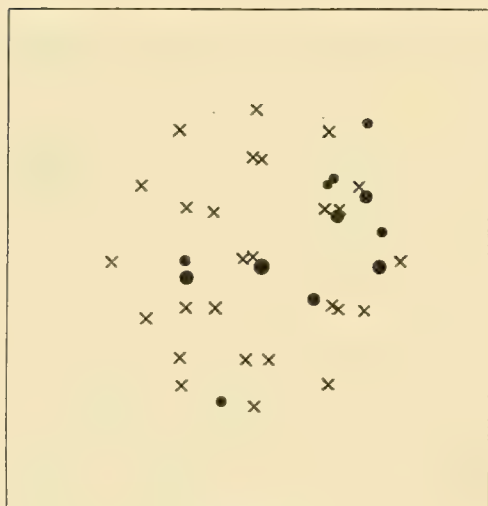


Figure 1.

## 2. Plate Material.

The longest exposure used was 30 min. or 1800 sec. In order to make it possible to measure all stars at about the same intensity of the image further exposures of 570, 180, 57, 18, 6 and 2 sec. were made.

The proportion between two consecutive exposures,  $(\sqrt{10})$  is nearly equal to  $19:6$ , corresponds to a difference in brightness of about 1 magnitude. The four shortest exposures were made successively on the same plate. Each series of exposures therefore consists of 4 plates. The brightest star, Alcyone, was taken as centre of the group. The positions of the centres of the separate fields are shown in Figure 1. The limits of this figure are the same as of the map given at the end of this paper. On each of the  $2 \times 7 = 14$  inner fields a series of 4 plates, as indicated above, was exposed. Of the  $12 + 1 = 13$  outer fields only one plate of 30 min. exposure time was taken. The programme comprised  $4 \times 14 + 12 = 68$  plates. To this was added one duplicate plate. Hence a total number of 69 plates was used. A catalogue of these 69 plates is given in Table 1.

As the diffraction images of higher order, especially of the brighter stars, are rather extended, neighbouring images occasionally overlap in one position of the grating and not in another. Accordingly the grating was used in two different orientations. On 1912 Aug. 10, Sept. 8, 9 and 11 and Oct. 16 the wires of the grating

Table 1.  
List of plates.

no. of plates	date	centre of field		sidereal time of exposure		efficiency of plate	deviation from mean	correction of $I_\lambda$ to the zenith	number of measured effective wavelengths
		$\alpha$ (1900) 3h	$\delta$ (1900)	middle	duration				
	1912	m	°	h	m	m	m	m	
53	Aug. 10	41.9	+23 50	1 26	1800	8.9	+1	—02	306
54	— —	42.0	23 50	1 51	57, 18, 6, 2	6.3, 4.9, 3.8, 2.8	+5	2	169
78	— 12	40.2	24 6	1 26	1800	9.1	+3	2	241
79	— —	40.2	24 6	1 50	570	8.2	+4	2	155
97	Sept. 8	42.6	24 4	1 29	1800	9.1	+3	2	218
98	— —	42.6	24 4	1 53	570	8.0	+2	2	134
99	— —	42.6	24 5	2 6	180	6.9	+1	1	80
100	— —	42.6	24 5	2 13?	57, 18, 6, 2	6.1, 4.9, 4.0, 2.9	+3	1	112
101	— —	42.6	23 36	2 31	1800	9.1	+3	0	258
102	— —	42.6	23 36	2 54	570	8.3	+5	0	180
103	— —	42.6	23 35	3 9	180	7.1	+3	0	101
104	— —	42.6	23 36	3 15	57, 18, 6, 2	5.9, 4.9, 4.0, 3.0	+1	0	143
105	— —	41.4	23 20	3 43	1800	9.1	+3	0	256
106	— —	41.3	23 20	4 7	57, 18, 6, 2	5.5, 4.6, 3.6, 2.0	—3	0	109
116	— 9	41.4	23 50	0 52	570	8.2	+4	4	145
117	— —	41.4	23 50	1 2	180	6.8	—0	3	100
118	— —	41.5	24 20	1 11	180	7.1	+3	2	82
119	— —	41.5	24 21	1 17	57, 18, 6, 2	5.8, 4.5, 3.9, 3.0	—0	2	98
120	— —	41.6	24 21	1 27	570	7.8	—0	2	124
121	— —	41.5	24 21	1 50	1800	9.0	+2	2	242
122	— —	39.9	23 35	2 14	57, 18, 6, 2	5.8, 4.9, 4.1, 2.8	—0	1	141
123	— —	39.8	23 36	2 21	180	6.9	+1	1	71
124	— —	39.8	23 36	2 30	570	8.0	+2	0	130
125	— —	39.8	23 35	2 53	1800	8.9	+1	0	229
126	— —	39.9	24 5	3 19	570	7.6	—2	0	140
127	— —	39.8	24 5	3 41	1800	8.8	—0	0	244
128	— —	39.9	24 5	3 59	180	7.2	+4	0	111
129	— —	39.9	24 6	4 4	57, 18, 6, 2	6.0, 4.9, 3.8, 2.8	+2	0	184
144	— 11	44.9	23 49	0 14	1800	8.6	—2	6	205
146	— —	43.3	24 29	1 31	1800	8.9	+1	2	247
147	— —	43.3	23 12	2 7	1800	8.3	—5	1	146
162	— 12	41.7	23 51	1 24	1800	8.7	—1	2	262
163	— —	41.8	23 50	1 48	570	7.4	—4	2	153
164	— —	41.8	23 50	1 57	57, 18, 6, 18, 2?	5.9, 4.9, 3.8, 4.7, 2.8	+1	2	205
165	— —	41.7	23 50	2 6	180	6.8	—0	1	98
166	— —	41.7	24 21	2 27	1800	8.8	—0	1	177
167	— —	41.7	24 20	2 49	570	7.7	—1	0	97
168	— —	41.7	24 21	2 59	180	6.6	—2	0	58
169	— —	41.7	24 21	3 4	57, 18, 6, 2	5.7, 4.4, 3.5, 2.5	—1	0	78
170	— —	41.9	23 20	3 24	1800	8.7	—1	0	198
171	— —	41.8	23 21	3 48	570	7.7	—1	0	112
172	— —	41.8	23 20	3 58	180	6.7	—1	0	64
173	— —	41.8	23 21	4 4	57, 18, 6, 2	5.8, 4.8, 3.5, 2.8	—0	0	108
174	— —	40.3	24 6	4 12	180	6.7	—1	0	74
175	— —	40.3	24 6	4 17	57, 18, 6, 2	5.6, 4.5, 3.8, 2.2	—2	0	146
215	Oct. 12	40.0	23 36	2 19	180	6.5	—3	1	58
216	— —	40.0	23 36	2 28	570	7.7	—1	0	92
217	— —	40.0	23 36	3 4	1800	8.5	—3	0	166
218	— —	40.1	23 36	3 24	57, 18, 6, 2	5.6, 4.6, 3.6, 2.2	—2	0	128
219	— —	43.2	23 36	3 40	570	8.3	—5	0	153
220	— —	43.2	23 35	3 49	180	6.8	—0	0	73



Table 1 (continued).

no. of plates	date	centre of field		sidereal time of exposure		efficiency of plate	deviation from mean	correction of $I_\lambda$ to the zenith	number of measured effective wavelengths
		$\alpha$ (1900) 3h	$\delta$ (1900)	middle	duration				
	1912	m	° ' "	h m	s	m	m	m	
221	Oct. 12	43.2	23 35'	3 56	57, 18, 6, 2	5.5, 4.8, 3.9, 2.9	—3	0	137
222	— —	43.2	23 35	4 14	1800	9.0	+2	0	232
223	— —	43.2	24 6	4 53	1800	8.5	—3	1	137
224	— —	43.2	24 5	5 9	180	6.8	.0	1	39
225	— —	43.3	24 3	5 18	570	7.6	—2	2	92
226	— —	43.2	24 4	5 27	57, 18, 6, 2	5.5, 4.5, 3.1, 2.1	—3	2	80
243	— 13	39.4	24 12	1 11	1800	8.8	.0	2	183
244	— —	39.3	23 35	1 51	1821	8.9	+1	2	136
245	— —	41.7	23 5	2 30	1800	8.7	—2	1	163
246	— —	41.7	24 35	3 10	1800	9.0	+2	0	203
247	— —	44.1	23 32	3 52	1800	8.5	—3	0	149
248	— —	44.2	24 12	4 32	1800	8.3	—5	0	149
305	— 16	40.1	23 12	2 20	1800	8.6	—2	1	124
306	— —	40.1	24 29	2 54	1800	8.6	—2	0	172
307	— —	38.5	23 50	3 30	1800	8.6	—2	0	125
310	— —	41.7	23 20	4 54	570	7.5	—3	1	88
311	— —	41.7	23 20	5 2	180	6.7	—1	1	62
312	— —	43.3	23 20	5 28	1800	8.5	—3	2	100
									9972

were placed parallel to the meridian, so that the diffraction images appear to the east and to the west of the central image, while on Aug. 12, Sept. 12 and Oct. 12 the grating was placed at right angles to this position.

The plates of the same exposure time do not all show images of the same intensity owing to differences in the transparency or quietness of the air or sensibility of the plates. To get a measure of the efficiency of the different plates, I have estimated on each plate the magnitude at which the spectra of the second order had a certain arbitrary intensity. The efficiencies thus found are given in stellar magnitudes (the zero point being arbitrary) for each plate separately in Table 1. Compared with the longest exposure of 1800<sup>s</sup> the exposures of 570<sup>s</sup>, 180<sup>s</sup> and 57<sup>s</sup> are in the mean respectively  $m.975 \pm m.054$  (m. e.),  $1m.973 \pm m.060$  and  $3m.054 \pm m.079$  less efficient. That is to say, that the proportion of exposure time chosen,  $\sqrt[3]{10}$ , practically corresponds to one magnitude. Hence for the plates used in this investigation the exponent  $p$  in the formula of Schwarzschild

$$\text{intensity of photographic image} = f (\text{intensity of light} \times \text{exposure time}^p)$$

is found to be  $.80 \pm .02$  (m. e.).

The mean efficiency of a plate is thus  $8m.8 + \log(t/1800)$ , where  $t$  is the exposure time in seconds. The deviations of the single plates from this formula are given in Table 1. The mean square  $m.062 = (\pm m.25)^2$  of these deviations gives a

measure for the dispersion of the apparent sensibility of the plates. The relative small efficiency of the later plates is striking.

The exposures have all been made by opening and closing the plateholder. For this reason the shortest exposure time,  $2^s$ , was rather uncertain and the different parts of the plate were not exposed exactly alike. But this circumstance is of no importance in the present case, because the intensity of each star image was estimated independently when the effective wavelength was measured.

### 3. The Measuring of the Plates.

The plates have been measured by the writer at Potsdam in the time from 1915 March 17 to Aug. 25. For this purpose the same Toepfer machine was used which has served for the measuring of my photographs of double stars (Potsdam Publ. Nr. 75). By this machine the displacement of the whole plate is measured micrometrically, which gives a guarantee for the constancy of the screw value.

The rectangular coördinates of the stars on each plate were noted to  $\frac{1}{10}$  of a mm. The diameter of the central star image was estimated to  $\frac{1}{100}$  of a mm by the aid of a double wire in the focal plane of the objective of the microscope.

On each plate the effective wavelengths were measured within a field, the diameter of which was  $1^\circ$ . This is a somewhat greater field than indicated above as fit for use and the star images near the border are rather unsharp. But in the present case, where several overlapping plates are available, the possible systematic differences between stars near to and far from the centre of the plate will to a great extent be compensated by taking the mean of the different plates, as usually the same star will on some plates be near to and on others far from the centre. Only the stars more than about  $1^\circ$  distant from Alcyone make an exception to this rule. — In other cases, where only plates with a common centre are available, it is not to be recommended to use a field greater than  $40'$  in diameter, when the reflector is diaphragmed down to an aperture of 1 meter.

The general appearance of the images is shown in Figure 2 for some stars of different brightness (Alcyone and neighbouring stars). The distance between the two spectra on each side of the central image was measured as between two star images. When the spectra were unsymmetrical it was aimed to place the wire in such a way that the area of the spectral image was cut into two equal parts. The setting was read to  $\frac{1}{2}\mu$  corresponding to about  $2\text{\AA}$  in the spectra of the first order or about  $^m01$  in the colour index.

When the thickness  $d$  of the wires of the grating is equal to the spare width  $l$  between them, all spectra of even order disappear, while, as stated above, those of uneven order are at their maximum intensity. For the grating here used  $d$  is only approximately equal to  $l$ . Hence the spectra of the second order also make their appearance in the images of bright stars. In fact we have  $d = 2.745$  mm and  $l = 3.255$  mm. Corresponding to the proportion  $l/d = 1.118$  the central image is

calculated to be  $1^m.33$  and the spectra of the first, second and third order respectively  $2^m.51$ ,  $6^m.88$  and  $5^m.05$  fainter than the star image as taken without the grating placed in front of the reflector. Owing to the oblong figure of the spectra the loss in limiting magnitude is still somewhat greater especially for the spectra of higher order. Here we are chiefly interested in the spectra of the first order, because they have the greatest intensity and the main point is to reach as faint stars

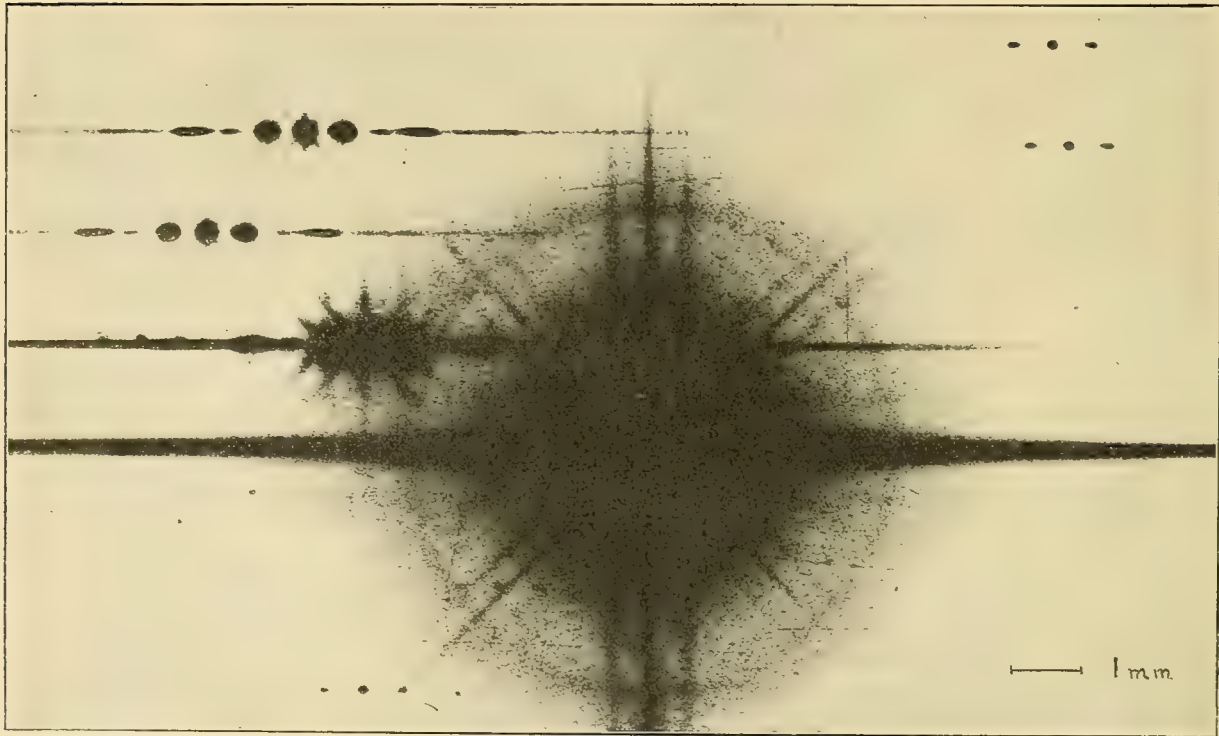


Figure 2.

as possible. The oblongness of the spectra of the first order varies sensibly with the seeing. The better the seeing is, the more oblong the spectra will appear. In the main we may say, that with the same exposure time the spectra of the first order reach about  $3^m$  less far than the stars taken without grating. Generally speaking we must choose the constant,  $d + l$ , of the grating by weighing the different points of view against each other. The smaller the constant of the grating is, the farther the spectra will be separated from each other and the same accuracy in measuring will consequently give a greater accuracy of the effective wavelength. But at the same time the spectra will get more oblong and less fit for accurate pointing, and possible systematic errors, caused by the unsymmetrical figure — varying with the definition — of the spectra, will be of more importance. Besides, the spectrum



fades out through its increased size, while we just want to reach as faint stars as possible. Partly to throw some light on these considerations I have measured not only the spectra of the first but also of the second and third order.

On each spectrum only one pointing was made. The gain in accuracy by repeated measurement of the same image is small in comparison with the other accidental and systematic errors. I therefore preferred to increase the accuracy by taking more plates.

In order to get a good determination of the variation of the effective wavelength and its mean error with the intensity of the image of the same star, also many faint images were measured which are individually of very little use.

#### 4. Reduction of the Effective Wavelengths to the same Intensity of the Image.

The determination of colour equivalents from effective wavelengths rests in the present paper on the supposition that the effective wavelength depends only on the colour of the star and the intensity of the image on the plate. Hence it is supposed that a bright and a faint star of the same colour will give the same effective wavelength when the exposure times are chosen in such a way, that the images of the two stars show the same intensity, or in other words, that the exponent  $p$  in the formula of Schwarzschild mentioned above is independent of the wavelength. The gradation of the scales of exposure time and of intensity may be different for different wavelengths, but the proportion between the two gradations must be independent of the wavelength. That the exponent  $p$  is practically independent of the wavelength has been found in different photographic investigations. As the part of the spectrum here considered is only small, the above assumption is plausible.

This assumption is, however, still supported by the material itself. The intensity of the spectra of the II<sup>nd</sup> order are, as mentioned above, 4.37 magnitudes fainter than the spectra of the I<sup>st</sup> order. If now two exposures of the same star are chosen of such different duration, that the spectra of the I<sup>st</sup> order of one exposure are of equal intensity as the spectra of II<sup>nd</sup> order of the other exposure, then practically the same effective wavelength is found from the spectra of the I<sup>st</sup> order of the short exposed and the spectra of the II<sup>nd</sup> order of the long exposed image. It may, of course, be objected that the spectra of I<sup>st</sup> and II<sup>nd</sup> order have different dispersion and are therefore not to be compared directly, but with spectra of approximately symmetrical figure appreciable errors are not to be expected on account of this circumstance. Another control was made by the aid of the faint diffraction images produced by the grating in connection with three metallic bars, which were placed at right angles to the rubber wires in order to support them at certain intervals and to keep them at the proper distances from one another. These additional spectra,

which can be seen on the image of Alcyone on Figure 2, are strongly eclipsed by the brightness of the main image and show a somewhat irregular figure owing to their inclined position. Still it may be noted as a support of the assumption made above, that also these additional spectra give practically the right effective wavelength, while they are about 9.7 magnitudes fainter than the common spectra of the 1<sup>st</sup> order. For the 5 brightest Pleiades these by-spectra gave on 42 images in the mean  $l = 1.054 \text{ mm} \pm .002 \text{ mm (m. e.)}$  or  $I_\lambda = -.30 \pm .04 \text{ (m. e.)}$  in comparison with  $-.20$  as found from the rest of the material. The difference  $.10 \pm .04 \text{ (m. e.)}$  is not too large. If anything, it would indicate a shortening of the effective wavelength for decreasing intensity of the light and correspondingly prolonged exposure time and that is exactly the opposite of what was feared.

The reduction of the measures was made in the following way. The distance in millimeters between the two spectra to the right and to the left of the central

Table 2.

Corrections to normal strength of the image, spectra of 1 <sup>st</sup> order, observed values.										
diameter of central image, $d$ .....	.05	.06	.07	.08	.09	.10	.11	.12	.13	.14 mm
mean correction of the effective wave- length to $d = .10 \text{ mm}$ }	12.0	10.5	5.7	4.4	1.9	0	-1.6	-3.8	-5.1	-5.9 $\mu$
number of differences used .....	125	171	330	418	164	—	120	400	220	131
diameter of central image, $d$ .....	.15	.16	.17	.18	.19	.20	.21	.22	.23	.24 mm
mean correction of the effective wave- length to $d = .10 \text{ mm}$ }	-6.7	-4.8	-7.6	-6.7	-7.3	-8.8	-8.2	-7.1	-4.8	-7.1 $\mu$
number of differences used .....	95	132	138	105	74	41	25	13	6	7

image, or the effective wavelength was first corrected to the zenith for selective extinction of the light in the earth's atmosphere. These corrections are given in Table 1 for each separate plate.

The intensity of the image on the plate was indicated by the diameter  $d$  of the central image of the star. As normal intensity was considered that for which the diameter of the central star image was  $\frac{1}{10} \text{ mm}$ . In that case the spectra are about 2 magnitudes stronger than the first visible traces and are therefore just well exposed.

It remained to find for a given star the variation of the effective wavelength with changing intensity of the spectra as shown on the plate. To this end for each star the differences of the observed effective wavelengths from that corresponding to a diameter  $d = .1 \text{ mm}$  of the central image were formed. The mean values of these deviations for different values of  $d$  are given in Table 2. No appreciable differences were found in these corrections for stars of different colour. The finally adopted smoothed corrections are given in Table 3. They have been applied to each separate effective wavelength.

Owing to a mistake the effective wavelengths derived from the spectra of the 1<sup>st</sup> order were treated separately for those exposures where also spectra of higher

order were of measurable intensity. For these effective wavelengths from the spectra of the 1<sup>st</sup> order new corrections to  $d = .1$  mm were derived. They are given in Table 4. It is seen, that for these usually very strong images no sensible variation of the effective wavelength with  $d$  was found. For these images I have therefore adopted the constant correction  $-12\mu$ . This correction is somewhat different from the one ( $-7\mu$ ) derived above for exposures of the same intensity. But it is evident, that there will be a systematic difference between the qualities of two images, showing the same diameter  $d$  of the central star, but in one case the spectra of

Table 3.

Corrections to normal strength of the image, spectra of 1<sup>st</sup> order, adopted values.

diameter of central image, $d$ .....	.05	.06	.07	.08	.09	.10	.11	.12	.13 m
adopted correction of the effective wavelength to $d = .10$ mm	+13	+10	+7	+4	+2	0	-2	-3	$-4\mu$
diameter of central image, $d$ .....	.14	.15	.16	.17	.18	.19	.20		.24 mm
adopted correction of the effective wavelength to $d = .10$ mm	-5	-6	-6	-7	-7	-7	-7		$-7\mu$

Table 4.

Corrections to normal strength of the image, spectra of 1<sup>st</sup> order, when spectra of higher order were also measured, observed values.

diameter of central image, $d$ .....	.13	.14	.15	.16	.17	.18	.19 mm
mean correction of the effective wavelength to $d = .10$ mm	-13.5	-17.2	-14.9	-9.6	-14.4	-11.2	$-12.3\mu$
number of differences used .....	3	4	5	10	24	40	38
diameter of central image, $d$ .....	.20	.21	.22	.23	.24	.25	.26 mm
mean correction of the effective wavelength to $d = .10$ mm	-11.0	-12.0	-12.8	-11.9	-12.2	-12.0	$-15.4\mu$
number of differences used .....	40	30	85	71	62	50	10

higher order measurable, and in the other not. In the latter case the images will be more nebulous (owing to unquietness of the air or great distance from the centre of the field) and this may give rise to systematic difference in the effective wavelength.

## 5. Precision of the Effective Wavelengths.

The effective wavelengths found for the same star from different plates showing exposures of the same intensity (same  $d$ ) were compared, and the mean error of a single effective wavelength derived from the differences between these values. The results are given in Table 5 and the adopted weights in Table 6.

As only one setting was made on each spectrum it is impossible to determine, which fraction of the square of the mean error is due to errors of pointing and which to defects of the image. In this respect my earlier paper (Potsdam Publ.



Nr. 63, p. 16, Tab. 8 and 9) may be compared. The mean errors here found are somewhat greater than those derived in case of the cluster *NGC* 1647 (Ap. J. **42**, 92; 1915). Part of this difference will at any rate be due to the fact that the plates of

Table 5.

Precision of effective wavelengths, spectra of I<sup>st</sup> order.

diameter of central image, $d$ . . . .	·05	·06	·07	·08	·09	·10	·11 mm
number of differences used . . . . .	82	125	222	254	246	211	165
square of mean error of $l$ . . . . .	843	428	281	138	89	57	61 $\mu^2$
weight of $I_\lambda$ . . . . .	3·0	5·9	9·0	18·3	28·4	45	41 $m^{-2}$
mean error of $I_\lambda$ . . . . .	$\pm 58$	$\pm 41$	$\pm 33$	$\pm 23$	$\pm 19$	$\pm 15$	$\pm 16 m$
diameter of central image, $d$ . . . .	·12	·13	·14, ·15	·16, ·17	·18, ·19	·20, ·21, ·22 mm	
number of differences used . . . . .	177	66	80	121	70	27	
square of mean error of $l$ . . . . .	44	40	54	64	39	33 $\mu^2$	
weight of $I_\lambda$ . . . . .	57	63	47	39	66	77 $m^{-2}$	
mean error of $I_\lambda$ . . . . .	$\pm 13$	$\pm 13$	$\pm 15$	$\pm 16$	$\pm 12$	$\pm 11 m$	

Table 6.

Adopted weights, spectra of I<sup>st</sup> order.

diameter of central image, $d$ . . . .	·05	·06	·07	·08	·09	·10	·11	·12	·13	·14 mm
adopted normal weight of $I_\lambda$ . . . .	2	4	8	18	28	38	48	56	58	52 $m^{-2}$
diameter of central image, $d$ . . . .	·15	·16	·17	·18	·19	·20	·21	·22	·23	·24 mm
adopted normal weight of $I_\lambda$ . . . .	44	36	28	22	16	12	18	6	4	2 $m^{-2}$

*NGC* 1647 were measured three times. The marked decrease in accuracy for the fainter images, formerly (Potsdam Publ. I. c.) found, is also shown by the present measures.

## 6. Determination of Approximate Magnitudes.

The estimates of the diameter  $d$  of the central star image were converted into provisional magnitudes according to Table 7, adding the constant of efficiency

Table 7.

diameter of central image, $d$ . . . .	·04	·05	·06	·07	·08	·09	·10	·11	·12	·13	·14	·15
provisional magnitude equivalent $m'$	7·0	6·5	6·1	5·6	5·2	4·8	4·5	4·1	3·8	3·5	3·2	2·9
$d$ . . . . .	·16	·17	·18	·19	·20	·21	·22	·23	·24	·25	·26	·27
$m'$ . . . . .	2·6	2·3	2·1	1·8	1·5	1·2	1·0	·7	·5	·3	·1	—·2
$d$ . . . . .	·28	·29	·30	·31	·32	·33	·34	·35	·36	·37	·38	·39
$m'$ . . . . .	—·4	—·6	—·8	—1·0	—1·2	—1·4	—1·6	—1·9	—2·1	—2·3	—2·5	—2·7
$d$ . . . . .	·40	·41	·42	·43	·44	·45	·46	·47	·48	·49	·50 mm,	
$m'$ . . . . .	—2·9	—3·2	—3·4	—3·6	—3·8	—4·0	—4·2	—4·4	—4·6	—4·8	—5·0	

given in Table 1 for each separate plate. The mean provisional magnitudes thus obtained for each star were finally reduced to the scale of A. N. 4767 by means of a table made according to the formula

$$m_{pr} = +12.239 + 1.008 (m - 12) - .017 (m - 12)^2$$

where  $m_{pr}$  is the provisional magnitude and  $m$  the definitive one.

The correction of  $m_{pr}$  to  $m$  is therefore zero at  $8^m.5$  and  $16^m.0$ . Its maximum value between these two magnitudes is  $-.m.24$  for  $m_{pr} = 12.2$ . There will however still remain systematic differences between stars near to and far from the centre of the plates. Near the border of the field bright stars have probably been estimated too bright, and faint ones too faint. The magnitudes are therefore supposed to be most reliable for stars less than  $40'$  distant from Alcyone. For this region I find by comparison with the magnitudes of A. N. 4767 the mean error to be about  $\pm .m.1$  at  $14^m$  and about  $\pm .m.2$  at  $15^m$ . Especially the faintest magnitudes are therefore uncertain even in the central region of the field investigated, but they are only meant to serve for Durchmusterung purposes.

## 7. The Coordinates.

The coordinates were noted to the tenth of a mm and converted into  $\alpha$  and  $\delta$  for 1900 for the following plates 53, 78, 105, 125, 127, 144, 146, 147, 243, 244, 245, 246, 247, 248, 305, 306, 307 and 312. The coordinates of a few stars not occurring on these plates have been added separately. For stars less than  $40'$  distant from Alcyone the mean error is in both coordinates about  $\pm 2''$ . For stars near the border of the field investigated it may be double this amount. This will be sufficient for the identification of the stars.

## 8. Spectra of the II<sup>nd</sup> Order.

For the reduction of the effective wavelengths derived from the spectra of the II<sup>nd</sup> order to normal intensity of the image I have not made use of the diameter  $d$  of the central star image, but the intensity of the spectra of the II<sup>nd</sup> order themselves was directly estimated on the plate. These estimates were made by estimating the diameter  $d'$  of the central star image for which the spectra of the I<sup>st</sup> order would have the same intensity as that actually observed for the spectra of the II<sup>nd</sup> order. With these equivalent diameters  $d'$  I then proceeded exactly in the same way as above with the diameter  $d$  referring to the spectra of the I<sup>st</sup> order. The approximate relation between  $d$  and  $d'$ , which for the rest is of no importance, is in the mean

$d = .24$	$.30$	$.36$	$.42$ mm
$d' = .084$	$.089$	$.100$	$.121$ mm.

When the diameter  $d$  of the central image is small, the spectra of the II<sup>nd</sup> order could only be measured when the air was quiet and the images consequently

sharp. For such images the intensity of the spectra of the II<sup>nd</sup> order, or  $d'$ , will be found comparatively high.

In order to make the comparison between the spectra of the I<sup>st</sup> and II<sup>nd</sup> orders as direct as possible,  $d' = .1$  mm was chosen to represent normal intensity of the spectra of the II<sup>nd</sup> order. For different values of  $d'$  the correction of the effective wavelength to  $d' = .1$  mm was found to be

$d'$ .....	.08	.10	.12	.134 mm
correction .....	+6.95	0	-7.1	-10.9 $\mu$
number of images $n$ .	74	—	43	26

After smoothing the following corrections were adopted

$d'$ .....	.08	.09	.10	.11	.12	.13	.14	.15 mm
corr. ....	+7	+3	0	-3	-7	-10	-13	-16 $\mu$

These corrections are, as was to be anticipated, about twice as large as those found for the distance between the two spectra of the I<sup>st</sup> order.

The mean error of a single effective wavelength from the spectra of the II<sup>nd</sup> order was determined in the same way as above for the spectra of the I<sup>st</sup> order. The values found are given in Table 8.

Table 8.  
Spectra of II<sup>nd</sup> order.

equivalent diameter of central image, $d' =$	.08	.09	.10	.11	.12	.13	.14 mm
number of differences used .....	97	185	98	61	22	7	1
square of mean error of distance between the spectra of II <sup>nd</sup> order	271	184	210	141	132	119	312 $\mu^2$
weight of $I_\lambda$ {							
observed .....	38	56	49	73	78	86	33 $m^{-2}$
smoothed .....	32	44	56	68	80	92	104 $m^{-2}$
adopted .....	8	32	56	64	56	32	8 $m^{-2}$

The spectra of the II<sup>nd</sup> order were measured on 703 images, the total weight of the corresponding colour indices being 26412  $m^{-2}$ .

## 9. Spectra of the III<sup>rd</sup> Order.

For the spectra of the III<sup>rd</sup> order a diameter  $d = .25$  mm of the central star-image was chosen as representing normal intensity of the exposure. For other values of  $d$  the adopted reductions to  $d = .25$  mm are contained in Table 9. In the same table the square of the mean error of the effective wavelength for different values of  $d$  is given followed by the smoothed weights, which have partly been further reduced on account of the uncertainty of the corrections to normal intensity of the image.



Table 9.  
Spectra of III<sup>rd</sup> order.

diameter of central image	adopted cor- rection of the effective wavelength to $d = \text{mm} \cdot 25$	number of differences used	square of mean error (m. e.) <sup>2</sup>	weight		
				observed	smoothed	reduced
mm	$\mu$		$\mu^2$	m <sup>-2</sup>	m <sup>-2</sup>	m <sup>-2</sup>
·14	+ 31	0	—	—	8	0
·15	+ 25	0	—	—	12	0
·16	+ 21	10	1008	23	16	2
·17	+ 18	4	736	31	22	4
·18	+ 15	18	762	30	27	8
·19	+ 12	16	311	74	33	14
·20	+ 10	34	592	39	39	22
·21	+ 8	9	355	65	46	31
·22	+ 5	50	464	50	53	42
·23	+ 3	26	410	56	59	52
·24	+ 2	56	369	63	63	61
·25	0	18	325	71	66	66
·26	— 1	30	201	115	68	67
·27	— 3	13	363	64	70	65
·28	— 5	20	303	76	70	60
·29	— 6	5	137	169	71	55
·30	— 8	22	508	45	71	48
·31	— 9	10	327	71	71	42
·32	— 11	26	234	99	72	36
·33	— 12	7	531	43	72	30
·34	— 13	32	444	52	72	25
·35	— 14	10	220	105	72	19
·36	— 16	24	177	131	73	15
·37	— 17	5	713	32	73	12
·38	— 18	22	339	68	73	9
·39	— 19	6	204	113	73	6
·40	— 20	16	274	84	73	3
·41	— 22	4	148	156	73	1
·42	— 23	3	423	55	73	0
·43	— 24	0	—	—	—	0
·44	— 25	1	312	74	—	0
·45	— 26	1	312	74	—	0

The spectra of the III<sup>rd</sup> order were measured on 1262 images, the total weight of the resulting colour equivalents being 45766 m<sup>-2</sup>.

## 10. Relation between Effective Wavelength and Colour Index.

As normal colour indices the  $I_H$  values of the Göttingen Actinometry were chosen. These  $I_H$  values are meant to represent the differences between the photographic Göttingen magnitude and the visual magnitude on the Harvard scale. In stead of simply giving the effective wavelengths in Ångström units, as I have previously done, I have in the present paper reduced them all to the  $I_H$  system of colour indices.

Table 10.

plate no.	date	centre of plate		sidereal time of exposure		correction of $I_k$ to the zenith
		$\alpha$	$\delta$	middle	duration	
	1912	h m		h m	s	m
231	Oct. 12	4 29	+ 15 $\frac{1}{2}$	6 43	114	—02.
234	— 13	19 32	+ 16	21 7	36	—02
235	— —	20 8	+ 12	21 22	360	—02
236	— —	19 45	+ 18	21 43	360	—02
238	— —	23 42	+ 3	22 44	360	—03
295	— 16	19 23	+ 20	21 0	114	—01.
298	— —	20 35	+ 13	22 3	114	—02
303	— —	0 44	+ 5	1 3	114	—02
330	— 17	4 13	+ 17	5 13	360	—01
331	— —	4 13	+ 17	5 27	360	—01.
332	— —	4 21	+ 15	5 42	360	—01.
333	— —	4 21	+ 15	5 56	360	—02
334	— —	4 25	+ 16	6 13	360	—02
335	— —	4 25	+ 16	6 26	360	—02.

Table 11.

plate no.	no. Potsdam Publ. Vol. 9	$BD$	phgr. magn. Göttingen	colour index $m_{pg}$ , Göttingen $m_p$ , Harv.	distance between spectra of 1st order reduced to $d = 1$ mm and to the zenith	relative weight of $l$	$O-C$
			$m_{pg}$	$I_H$	$l$	$p$	$(I_H)$
			m		mm	m <sup>-2</sup>	m
295	2766	+19°4019	6.39	—22	1.0736	480	—33
295	2764	19°4015	5.47	—10	1.0858	370	—44
234	2800	15°3866	6.88	—01	1.0443	500	+44
295	2759	19°4009	6.17	—00	1.0707	366	—05
295	2757	19°4004	7.20	—17	1.0726	342	+08
334, 335	541	15° 637	5.02	—21	1.0834	198	—09
334, 335	539	15° 636	5.93	—22	1.0720	36	+14
332, 333	512	15° 625	4.84	—23	1.0875	296	—14
298	3040	12°4405	7.85	—26	1.0757	448	+11
231	549	15° 645	6.36	—29	1.0825	30	+01
334, 335	544	15° 640	6.93	—33	1.0853	246	—00
334, 335	542	15° 639	5.84	—36	1.0866	56	+00
332, 333	509	15° 621	6.95	—44	1.0781	200	+24
234	2814	15°3877	7.61	—47	1.0881	192	+08
334, 335	532	15° 633	7.13	—49	1.0918	240	+03
303	80	4° 123	6.56	—73	1.1211	434	—28
330, 331	498	17° 712	4.98	—81	1.1152	146	—09
295	2760	19°4010	6.21	—94	1.1233	334	—12
334, 335	528	15° 631	5.05	—98	1.1162	182	+06
334, 335	525	16° 605	6.31	1.04	1.1288	236	—12
234	2816	16°3918	6.73	1.06	1.1175	496	+12
234	2805	16°3902	8.59	1.20	1.1172	156	+26
235	2954	11°4180	7.88	1.22	1.1308	106	+02
236	2848	18°4240	5.32	1.23	1.1305	36	+04
295	2765	19°4017	7.47	1.35	1.1485	514	—18
298	3047	12°4419	8.71	1.42	1.1431	458	—01
298	3042	12°4411	7.47	1.59	1.1443	486	+14
238	3486	2°4709	7.64	2.10	1.1742	246	+08

For the determination of the relation between effective wavelength and colour index  $I_H$ , 14 special plates were taken of stars contained in the Göttingen Actinometry. The data of these plates are given in Table 10 and the results of the separate stars in Table 11. Least square solutions gave the following formulae using first the colour index  $I_H$  and then the effective wavelength  $l$  measured in millimeters as argument:

$$l - 1.10317 = .04983 (I_H - .672)$$

and

$$I_H - .672 = 19.033 (l - 1.10317)$$

The effective wavelength in Ångström units is equal to  $3944.2l$ . Hence

$$\Delta \lambda_{\text{eff}} / \Delta I_H = 197 \text{ and } 207 \text{ or in the mean } 202 \text{ Å}/m \pm 13 \text{ Å}/m (\text{m. e.})$$

Finally the value  $\Delta \lambda_{\text{eff}} / \Delta I_H = 200 \text{ Å}/m$  has been adopted, or

$$\begin{aligned} I_H &= 19.721 (l - 1.0690) \\ \lambda_{\text{eff}} &= 200 I_H + 4216.4 \end{aligned}$$

For the colour index derived from the effective wavelength the designation  $I_\lambda$  is used.

## 11. Relation between the Effective Wavelengths found from the Spectra of the I<sup>st</sup>, II<sup>nd</sup> and III<sup>rd</sup> Order.

The effective wavelengths found from the spectra of the II<sup>nd</sup> and III<sup>rd</sup> order were first converted into provisional values of  $I_\lambda$  by the aid of the formula derived for the spectra of the I<sup>st</sup> order. Marking these provisional values with ' the following relations were found empirically:

$$\begin{aligned} I_{\lambda, \text{I}} &= +.020 + .632 I'_{\lambda, \text{II}} + .1044 I'^2_{\lambda, \text{II}} \\ \text{and} \quad I_{\lambda, \text{I}} &= -.084 + .617 I'_{\lambda, \text{III}} + .1482 I'^2_{\lambda, \text{III}} \end{aligned}$$

These formulae were used for the reduction of  $I'_{\lambda, \text{II}}$  and  $I'_{\lambda, \text{III}}$  to the system  $I_{\lambda, \text{I}}$  adopted in the present paper.

## 12. Detailed Example of the Measures of Star No. 508.

It was at first intended to print for each star the effective wavelength derived from each separate exposure. For obvious reasons this idea has been abandoned. The example given in Table 12 of the measures of the star no. 508, the  $6\frac{1}{2}^m$  distant companion to Alcyone, will be sufficient to show the character of the observations. The first 4 columns of Table 12 refer to the spectra of the I<sup>st</sup> order, the next 4 columns to those of the II<sup>nd</sup> order and the last 4 columns to those of the





III<sup>rd</sup> order. The measures of the spectra of the I<sup>st</sup> order are divided into two groups according to the description given above. For each image the number of the plate is followed by the diameter  $d$  or equivalent diameter  $d'$  of the central image given to hundredths of a millimeter. Then follows the measured distance between the two spectra corrected to normal intensity (denoted by  $d$  or  $d'$ ) of the image. Finally the weight of the effective wavelength is given, unit weight corresponding to a mean error of  $\pm 1^m$  in the equivalent colour index  $I_\lambda$ . Half the normal weight was given to images of inferior quality. This star here chosen as an example is, of course, one of those where the number of measured effective wavelengths is largest.

### 13. Other Determinations of Colour Equivalents of Stars in the Pleiades.

In Table 13 I have compared the effective wavelengths, obtained from the Mount Wilson plates, with colour equivalents from other sources all reduced to the scale of  $I_\lambda$  used in the present paper.

The first part of Table 13 contains the 300 Gaultier stars, which comprise the stars brighter than about  $13^m.5$  photographically within  $55'.4$  of the central star Alcyone. A few bright stars outside this field are given in the second part of Table 13.

The different sources of supplementary colour equivalents used in forming mean values of  $I_\lambda$  are:

1. Effective wavelengths for 59 stars from plates taken with a 81 mm refractor ( $f = 1236$  mm) at the Urania observatory, Copenhagen (Potsdam Publ. 63, Table 13).

2. Colour indices for 19 bright Pleiades using the photographic magnitude given in the Göttingen Actinometry (Teil B, Abh. der Ges. der Wiss. zu Göttingen, Math.-phys. Klasse, Neue Folge, Bd. 8, Nro. 4, 14; 1912) in combination with the visual Harvard magnitudes.

3. Colour indices for 92 stars, using the Potsdam UV Zeisstriplet photographic magnitudes combined with the visual magnitudes of Müller and Kempf (A. N. 3587, Bd. 150, 193; 1899).

4. Colour indices for 234 stars estimated photographically by TIKHOFF (Publ. de l'Obs. Centr. Nicolas, Sér. 2, Vol. 17) comparing on an arbitrary magnitude scale the differences between the wavelengths 540 and  $425 \mu\mu$ .

### 14. Relation between Brightness and Colour of the Physical Members and Hypothetical Parallaxes of the Pleiades.

A complete separation of the physical members of a cluster from other stars projected on the field investigated is not possible, because it may always happen, that stars not belonging to the group have proper motions (and radial velocities) agreeing within the errors of observation with the motion of the cluster. It is there-









Table 13 (continued.)

Gautier no.	Mount Wilson effective wavelengths from spectra of the order						Copenhagen effective wavelengths Potsdam Publ. 63	Göttingen actinometry and Har- vard, vis.	UV Zeiss- triplet and Müller and Kempf visual	Tikhoff difference between 425 and 540 $\mu\mu$	weighted mean			
	I		II		III									
	$I_\lambda$	$p$	$I_\lambda$	$p$	$I_\lambda$	$p$						$I_\lambda$	$p$	$I_\lambda$
	m	m-2	m	m-2	m	m-2	m	m-2	m	m-2	m	m-2	m	m-2
151	1.18	944							1.05	31	1.12	83	1.17	1058
152	.78	677									.89	63	.79	740
153	.64	820									.54	68	.63	888
154	.39	754									.49	64	.40	818
155	.89	446			.91	400			.89	200	.92	145	.90	1191
156	.27	191											.27	191
157	.53	312									.57	78	.54	390
158	1.03	598									1.12	60	1.04	658
159	.26	1080			.28	266			.27	190	.23	143	.26	1679
160	1.10	172											1.10	172
161	1.12	436							1.11	61	1.17	91	1.13	588
162	.38	892									.49	69	.39	961
163	.43	484							.48	44	.54	74	.45	602
164	.28	344											.28	344
165	1.31	267									1.46	92	1.35	359
166	.30	868			.36	253			.24	167	.40	137	.31	1425
167	1.27	696									1.23	63	1.27	759
168	.27	639									.52	68	.29	707
169	.30	478									.11	85	.27	563
170	1.46	272	1.42	276	1.45	298	1.30	285	1.51	410			1.43	1541
171	.52	540									.79	43	.54	583
172	.76	326							.80	84	.90	97	.79	507
173	.29	811			.26	367			.21	280	.29	169	.27	1627
174	.31	184											.31	184
175	.41	442									.60	48	.43	490
176	.41	340											.41	340
177	.20	1134			.14	998	.06	223	.22	450	.12	212	.17	3017
178	.30	268									.48	56	.33	324
179	1.01	355									.91	43	1.00	398
180	.33	888			.41	58			.34	118	.45	121	.35	1185
181	.19	537			.29	140			.25	150	.39	131	.24	958
182	.30	472									.35	69	.31	541
183	1.01	340									.89	43	1.00	383
184	.37	251											.37	251
185	—20	224	—17	256	—15	379	—18	1746	—18	300	—24	1150	—16	127
186	.26	430									.31	96	.27	526
187	.28	177											.28	177
188	.17	728									.13	68	.17	796
189	.28	897			.36	173			.23	158	.25	138	.28	1366
190	.40	563									.52	66	.41	629
191	.07	1200	.04	1072	.05	1028	.05	1001	.09	740	.08	245	.06	5286
192	.98	696									1.17	63	1.00	759
193	.25	702	.18	8	.23	588	.43	3	.19	310	.25	179	.23	1790
194	.35	523									.40	122	.36	645
195	1.34	543									1.40	53	1.35	596
196	.36	502									.49	65	.37	567
197	.42	393									.60	50	.44	443
198	.19	660									.16	66	.19	726
199	.39	113											.39	113
200	1.34	326									1.28	34	1.33	360





Table 13 (continued.)

Gautier no.	Mount Wilson effective wavelengths from spectra of the order						Copenhagen effective wavelengths Potsdam Publ. 63	Göttingen actinometry and Har- vard, vis.	UV Zeiss- triplet and Müller and Kempf visual	Tikhoff difference between 425 and 540 $\mu\mu$	weighted mean	
	I		II		III							
	$I_\lambda$	$p$	$I_\lambda$	$p$	$I_\lambda$	$p$	$I_\lambda$	$p$	$I_\lambda$	$p$	$I_\lambda$	$p$
251	m	m-2	m	m-2	m	m-2	m	m-2	m	m-2	m	m-2
252	—	—	·16	96	·16	116	·10	295			·10	220
253	—11	316	—13	408	—12	389	—16	1536	·03	300	—10	192
254	·68	256									·66	43
255	1·33	622							1·42	64	1·26	94
256	·13	456									·26	80
257	·47	492									·38	76
258	·66	492									·61	62
259	·45	164									·67	42
260	·35	284										
261	·37	238										
262	·08	549	—08	8	·04	642	·01	31			·06	187
263	1·19	301							·03	350	·13	95
264	—01	290	·05	400	—01	423	·00	652	1·15	61	·05	236
265	·31	114							·04	630		
266	·20	404			·16	110					·24	137
267	·30	258										
268	—06	262	—04	432	—07	267	—03	1140	·03	300		
269	·23	340										
270	·32	73										
271	·21	212									·38	59
272	·32	550									·45	78
273	1·10	155									·87	34
274	·89	552									·83	71
275	·99	482									·97	60
276	·26	262									·25	81
277	·02	194	·02	8	·07	235	·03	1	·11	300	·11	172
278	·16	163									·28	48
279	·48	214									·44	84
280	·30	196										
281	1·24	202									1·09	45
282	·10	177	·06	320	·02	308	·10	547	·03	640	·03	237
283	·94	198									1·09	49
284	·25	306									·36	85
285	·31	284									·47	77
286	·29	77										
287	·14	296									·25	96
288	·44	246									·44	97
289	·20	302									·31	59
290	·37	158										
291	·31	250									·39	117
292	·34	60										
293	·98	184									·86	75
294	·50	84										
295	·32	55										
296	·03	108	·09	216	—04	134	·05	1050	·01	780	—05	245
297	·74	268									·77	58
298	·95	253										
299	1·19	158									1·04	94
300	1·12	70									1·01	35
	·59	55										

Table 13 (continued.)

no. general catalogue	Mount Wilson effective wavelengths from spectra of the order						Copenhagen effective wavelengths Potsdam Publ. 63	Göttingen actinometry and Har- vard vis.	UV Zeiss- triplet and Müller and Kempf visuai	Tikhoff difference between 425 and 540 $\mu\mu$	weighted mean	
	I		II		III							
	$I_\lambda$	$p$	$I_\lambda$	$p$	$I_\lambda$	$p$						
8	m	m-2	m	m-2	m	m-2	m	m-2	m	m-2	m	m-2
27	-06	4	-12	32	-17	60					-17	60
29					-01	52					-11	36
65	-17	176							-51	51	-01	52
108	-19	111			-15	106					-25	227
123					-05	65					-17	217
165	-24	2			-77	61					-05	65
169					-21	132					-75	63
182					-41	60					-21	132
248			-03	112	-08	3			-26	190	-41	60
260	-14	12			-12	84					-15	305
269	-09	262			-06	117					-12	96
310					-44	120					-08	379
328	-77	28			-73	14					-44	120
396					-04	133					-76	42
416	-19	153			-03	14					-04	133
480	-88	6			1-09	42					-18	167
526			-04	32	-08	30					1-06	48
600			-11	8	-09	36					-06	62
695	-09	2			-24	127					-09	44
724					-63	60					-24	129
1088	-29	45			-28	36			-12	153	-63	60
1158					-07	182					-18	234
1164	-96	75			-96	42					-07	182
1184					-11	108					-96	117
1224	-30	18			-32	22					-11	108
											-31	40

fore more or less arbitrary, which stars are counted as members of the group, while for a number of stars with distinct different motion it may be taken for certain that they do not belong to the system. In the case of the Pleiades the picking out of the physical members is difficult because the proper motion of the group is small and directed nearly away from the sun's apex. According to the *PGC* of Lewis Boss the mean proper motion of 12 bright stars in the Pleiades is  $''^a.054$  in the direction  $158^\circ$  or, applying the Kapteyn correction of  $+''^a.013 \cos \delta$   $= ''^a.012$  to the proper motion in declination (B. A. N. 14),  $''^a.043$  in the direction  $152^\circ$ . The direction from the sun's apex is  $147^\circ$ . It is therefore possible, that the Pleiades, after correction for the sun's motion, are practically at rest in space. The radial velocity calculated under this assumption is  $+8 \text{ km/s}$  in accordance with the observed mean value  $+8 \text{ km/s} \pm 2 \text{ km/s}$  (m. e.) (comp. JOHANNES JUNG, *Astron. Mitt. der Sternw. zu Göttingen*, No. 17; 1914). If the apparent proper motion of the Pleiades is considered as entirely caused by the motion of our sun, being  $19 \text{ km/s}$ , the



parallax of the Pleiades is calculated to be "0147 according to the proper motion of Boss or "0119 after having applied the Kapteyn correction.

If the relative proper motions of the Pleiades (also some unpublished material was used for this purpose) are plotted separately for each magnitude, it is seen that the stars of the 4 or 5 brightest magnitudes nearly all belong to the system. The diagram containing the stars between the photographic magnitudes  $10^m$  and  $11^m$  still markedly shows that a group of these stars is moving with the cluster, while there is no more evidence of this when we consider stars between  $11^m$  and  $12^m$ . Regarding still fainter stars there are hardly more objects showing a proper motion common to that of the Pleiades, than should be expected by accident. The good agreement of the colours of such fainter stars, apparently sharing the motion of the cluster, with those expected, is deceiving, because these colours will also be about normal for faint stars of such proper motions which are not members of the system. It is thus very probable that R. TRÜMLER (Lick Bull. 333, Vol. 10, 110; 1921) has overestimated the number of faint stars belonging physically to the group.

I have therefore found it safest, until more accurate proper motions are available, to confine myself to stars brighter than  $11^m$  photographically when trying to separate the members of the system from the rest. A list of 66 stars thus considered as physically belonging to the group of the Pleiades is given in Table 14. The most remarkable fact shown by this table is the very regular change in colour with the magnitude. Between  $4^m.5$  and  $11^m$  the relation between  $I_\lambda$  and  $m_{pg}$  is nearly linear. A least square solution gave for these stars the formula

$$I_\lambda = -0.662 + 0.0945 m_{pg}$$

The deviations  $O-C$  in  $I_\lambda$  are given in the fourth column. Their smallness is a sign of the accuracy of the  $I_\lambda$ -values. As there may be a slight preponderance of positive values of  $O-C$  in the neighbourhood of  $8^m$  I have compared the  $O-C$  values of two consecutive stars in the magnitude sequence in order to determine the accuracy with which the colour or  $I_\lambda$  value of a star may be predicted by its magnitude. Taking the mean error of the determination of  $I_\lambda$  into account, it is found that the mean "error" or deviation of  $I_\lambda$  from the normal value for a given magnitude is  $\pm 0.028$ . To that degree therefore members of the Pleiades of the same magnitude have the same colour index. It is to be remembered, that double stars counted as single and consisting of two nearly equal components should give  $O-C$  values about  $+0.09$  greater than for single stars.

The 10 stars brighter than  $5^m.5$  are all practically of the same colour, the deviations from the mean  $I_\lambda = -0.20$  not being greater than the observational errors  $\pm 0.015$ .

For the physical members of the group of the Hyades I have formerly (A. N. 5000, Bd. 209, 120; 1919) found the relation  $I - 0.364 = 0.0935 (m_{pg} - 6.596)$ . The coefficient  $\Delta I / \Delta m_{pg}$  is thus practically the same, viz.  $+0.094$ , for the Hyades and

Table 14.

Gaultier no.	phgr. magn.	$I_k$	$O-C$	weight $p$	Gaultier no.	phgr. magn.	$I_k$	$O-C$	weight $p$
	m	m	m	$m^{-2}$		m	m	m	$m^{-2}$
144	2.82	—18	(+22)	4925	8	8.21	+15	+04	1121
219	3.53	—22	(+11)	4944	227	8.34	+11	—02	3046
38	3.57	—21	(+11)	4391	27	8.38	+14	+01	1717
71	3.80	—20	(+10)	4612	99	8.44	+20	+06	2244
90	4.13	—19	(+08)	5154	132	8.48	+14	—00	3913
49	4.18	—22	(+05)	3701	204	8.59	+16	+01	1048
224	4.94	—19	+01	5052	177	8.60	+17	+02	3017
185	5.30	—19	—03	4182	121	8.63	+15	—00	3466
34	5.37	—18	—03	4536	118	8.66	+19	+03	2089
46	5.49	—21	—07	3263	59	8.87	+17	—01	1624
76	5.69	—13	—01	4608	44	8.90	+16	—02	1766
252	6.04	—12	—03	4101	126	9.00	+23	+04	2891
133	6.31	—02	+05	6263	45	9.28	+11	—10	1223
78	6.37	—11	—05	4631	24	9.43	+22	—01	1525
236	6.56	—09	—05	4749	193	9.46	+23	—00	1790
113	6.76	—05	—03	5655	104	9.67	+21	—04	2055
267	6.77	—03	—01	2401	173	9.69	+27	+02	1627
145	6.84	+01	+03	5609	66	9.85	+23	—04	1556
134	6.95	—00	+01	5400	53	10.23	+19	—11	455
295	7.00	+03	+03	2533	159	10.29	+26	—05	1679
191	7.03	+06	+06	5286	65	10.33	+29	—02	402
63	7.24	+04	+02	3764	64	10.40	+24	—08	1086
137 A	7.28	—01	—04	948	189	10.43	+28	—04	1366
94	7.44	+08	+04	5107	137 B	10.53	+37	+04	473
281	7.52	+06	+01	2129	181	10.60	+24	—10	958
263	7.59	+02	—04	2631	62	10.67	+30	—05	1147
231	7.60	+06	—00	3895	266	10.69	+30	—05	258
135	7.85	+12	+04	4099	103	10.73	+52	+17	1225
141	7.86	+10	+02	4049	194	10.82	+36	—00	645
73	7.99	+13	+04	3107	84	10.86	+35	—01	453
239	8.10	+08	—02	3180	180	10.86	+35	—01	1185
86	8.19	+14	+03	3014	290	10.95	+34	—03	367
56	8.21	+13	+02	2573	102	10.98	+28	—10	398

the Pleiades. It is therefore of interest to see what is the constant difference of magnitude between stars of the same colour in the Pleiades and the Hyades.

According to B. A. N. 35 the 5 Pleiades Gaultier 90, 49, 224, 185 and 34 have the mean photographic magnitude  $4^m.882$  and the mean  $c_2/T$  value  $1.576$ , while the corresponding values for the 10 stars H. R. 1473, 1387, 1392, 1394, 1620, 1479, 1427, 1444, 1380 and 1388 belonging to the Hyades are  $m_{pg} = 4^m.865$  and  $c_2/T = 1.976$ . For stars of the apparent photographic magnitude  $4^m.87$  therefore  $c_2/T$  is .40 greater for the Hyades than for the Pleiades corresponding to  $\Delta I_k = .24$ . Comparing the same 5 Pleiades as just mentioned with the 7 Hyades H. R. 1389, 1473, 1394, 1479, 1444, 1427 and 1380 the mean photographic magnitude according to the Göttingen Actinometry is in both cases  $4^m.81$  and the mean value of  $H' = 6 + (H - 6)/1.02$ , where  $H$  is the visual Harvard magnitude (comp. A. N. 5000, 118), is  $4^m.97$  in the case of the Pleiades and  $4^m.66$  in the case of the Hyades, thus giving a difference in colour index of  $.31$ . The mean of the two values for this difference  $.24$  and

$m_{31}$  is  $m_{263}$  giving double weight to the former. For the 5 Pleiades considered, the mean value of  $I_\lambda$  is  $-1.96$ , and for the Hyades of magnitude  $4^m.865$  it is thus found to be  $-1.96 + .263 = +.067$ . This value of  $I_\lambda$  corresponds to  $m_{pg} = 7.54$  in the Pleiades. Hence, the magnitude difference between stars of the same colour in the Pleiades and the Hyades is  $7^m.54 - 4^m.865 = 2^m.675$ . Supposing that stars of the same colour have the same absolute magnitude in the two groups and adopting a parallax of  $''0.027$  for the Hyades (A. N. 5000, 114) the parallax of the Pleiades is calculated to be  $''0.0079$ .

For the 6 stars  $\beta, \gamma, \delta, \epsilon, g$  Ursae majoris and  $\alpha$  Coronae borealis of the Ursa major system the mean photographic magnitude is  $2^m.74$ , the mean value of  $c_3/T$  is  $1.72$ , and the mean parallax  $''0.043$ . The same colour is found for Pleiades of the photographic magnitude  $6^m.17$  differing by  $6^m.17 - 2^m.74 = 3^m.43$  from the mean magnitude of the 6 stars of the Ursa major system. From these data the parallax of the Pleiades is in the same way as above calculated to be  $''0.0088$ . The two results  $''0.0079$  and  $''0.0088$  agree with the first estimate made of the parallax of the Pleiades by a reasoning of this kind, using the spectral classification of Antonia C. Maury, viz.  $''0.0085 \pm ''0.002$  (m. e.) (Zeitschr. für wiss. Photographie Bd. 5, 106, footnote 37; 1907).

Orbital motions in double stars physically belonging to the Pleiades are so far too inaccurately known to allow of a reliable calculation of hypothetical dynamical parallaxes.

Taking the parallax of the Pleiades to be  $''0.009$ , a distance of one parsec inside the group corresponds to an angle of  $57^\circ.3 \times .009 = 0.52$  or  $31'$  as seen from the earth. The number of Pleiades with a space distance from Alcyone of less than one parsec may be estimated at about 50 or about 150 times larger than the star density in the neighbourhood of our sun (comp. B. A. N. 5, 21; 1922). The corresponding proportion of mass is probably a few times greater, while the total light intensity of the stars per unit volume in the inner region of the Pleiades is about 4000 times larger than in the neighbourhood of our sun. It therefore appears that the conspicuousness of the Pleiades as seen in the sky is due partly to great star density inside the group and partly to great luminosity of its members and that the importance of these two causes is of the same order of magnitude.

## 15. The Colours of Stars not Physically belonging to the Pleiades.

In Figure 3 a diagram is given containing the 421 stars, for which the weight of  $I_\lambda$  is at least  $100 m^{-2}$ . (Adding the colour indices of Shapley and Richmond this number would be increased with 28 to 449). Stars with a proper motion approximately equal to that of the group are indicated by crosses, the other stars by dots. Probably not all the stars marked with a cross and fainter than the 12<sup>th</sup> photographic magnitude are physically connected with the cluster.



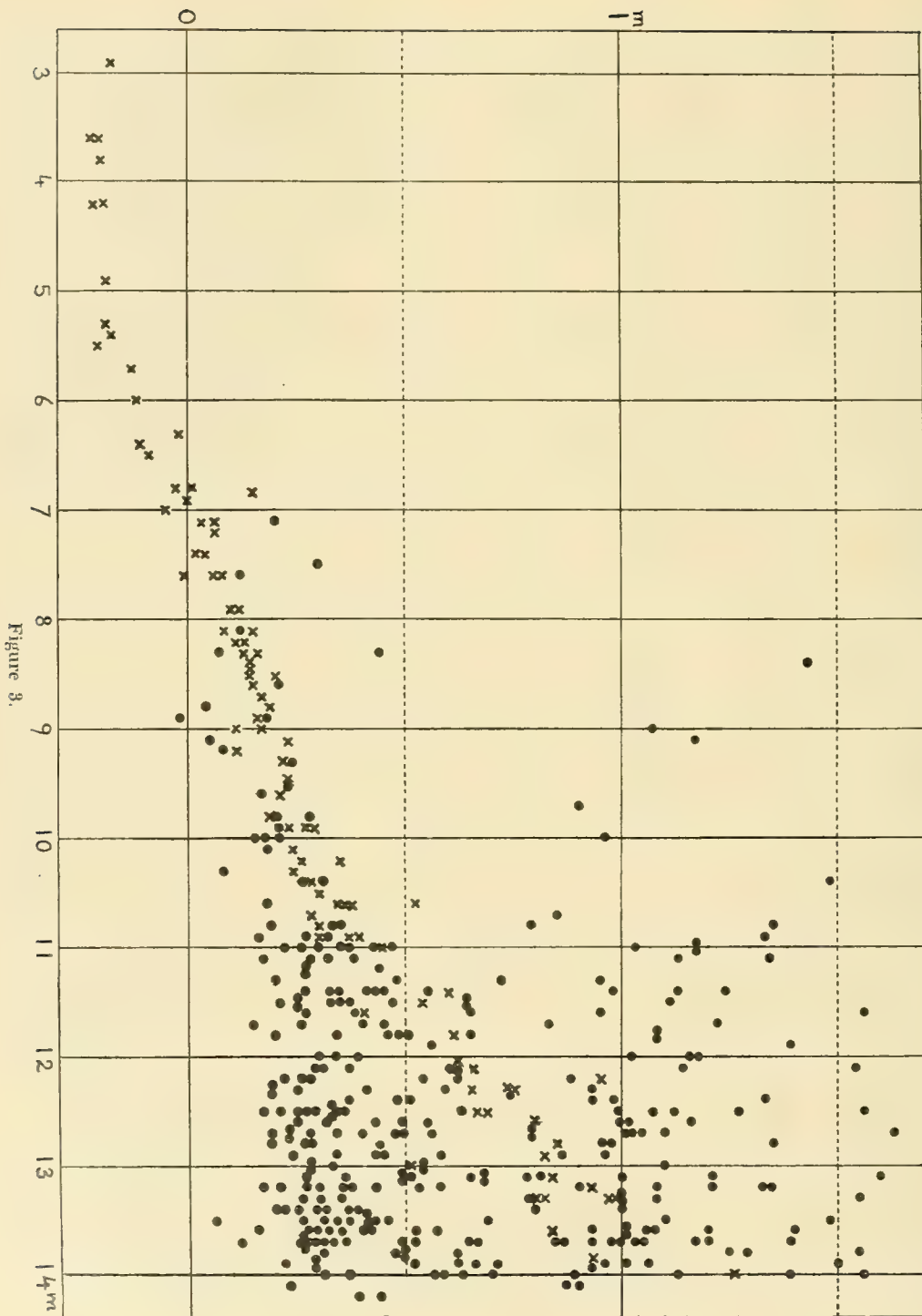


Figure 3.

The colours of the 236 stars for which  $m_{pg} > 11^m.95$  and  $p(I_\lambda) > 99.5 m^{-2}$  are distributed as follows

limits of $I_\lambda$ . . . . .	·0	·1	·2	·3	·4	·5	·6	·7			
number of stars . .	1	7	36	34	22	18	19				
	·7	·8	·9	1·0	1·1	1·2	1·3	1·4	1·5	1·6	1·7
	10	13	21	19	9	7	6	2	6	1	

In Figure 4 the full curve represents the smoothed relative frequencies of  $I_\lambda$  for these faint stars of mean photographic magnitude  $13^m$  forming the background of the Pleiades cluster. For comparison the corresponding curves are shown firstly for the 103 stars in the whole sky which are brighter than  $3^m$  photographically according to King (Harv. Ann. 71, 21 and 76, 117), broken line, and secondly for

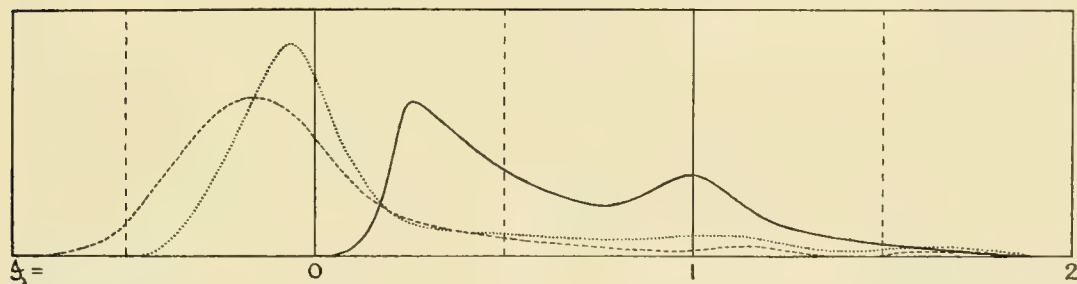


Figure 4.

the 136 stars north of the equator and brighter than  $4^m$  photographically (Leiden Ann. 14, II), dotted line. The bad agreement between these two additional curves may be mainly due to unreliability of the material used. At any rate the difference in the colour distribution shown by stars of  $m_{pg} = 13^m$  in the Pleiades and of  $m_{pg} = 3^m$  taken from the whole sky is very striking. This difference may, as is well known, be explained without assumption of selective extinction of light in space, simply by the falling off in star density with increasing distance from our sun thus causing a lack of absolutely bright and white stars among the apparently faint stars.

## 16. Double and Neighbouring Stars.

In Table 15 the 33 more conspicuous pairs of stars, noted during measurement of the plates, have been listed. The narrowest of these pairs (no<sup>s</sup> 408 and 407) shows a distance of  $1''.5$  between the two components, while among the following double stars, which were not recognized as double on the plates, is one of about  $1''.6$  separation.

gen. cat. no.	Gaultier no.	Bu		distance	$m_{pg}$ m	$I_{\lambda}$ m	$p$ $m^{-2}$
74	21	1838	Barnard 3	1'6	11'0	47	539
248	—	1853	$\Sigma$ 444	3'3	5'8	15	305
313	86	1856	$\beta$ 536	2	8'4	14	3014
447	118	1866	$\beta$ 537	4	8'8	19	2089
757	193	1883	$\beta$ 1105	3	9'5	23	1790
870	219	1887	$\Sigma$ 453	4?	3'6	22	4944
1020	271	1898	$\beta$ 1106	4	11'8	34	628

$\Sigma$  444 was not seen double because it only occurs on long exposed plates and near the border of the field.

Table 15.  
Double and neighbouring stars.

number in general catalogue		A		photogr. magnitude		A		B		pos. angle	dis- tance	plate no.
A	B	$\alpha$ (1900) 3h	$\delta$ (1900)	A	B	$I_{\lambda}$	$p$	$I_{\lambda}$	$p$	$\theta$	$\varrho$	
		m s	° ' "	m	m	m	$m^{-2}$	m	$m^{-2}$			
20	21	37 38.0	+24 16 33	14.2	15.2	1.38	4	.89	1	170.6	17.70	243
73	71	38 17.1	23 42 53	12.1	12.7	.61	280	.79	220	310.4	5.67	244
221	224	39 43.5	24 8 41	13.9	14.9	.23	71	.39	6	132.1	2.61	78
273	278	40 8.9	24 15 17	13.9	14.9	1.06	124	1.40	21	161.5	17.58	78
305	306	40 17.0	23 53 3	9.1	13.8	1.17	2183	.32	92	7.8	18.20	127
368	373	40 38.6	23 39 3	12.0	15.5	.30	931	.74	3	32.9	23.11	53
401	402	40 46.7	23 56 41	14.2	15.3	.55	94			34.9	3.06	53
408	407	40 48.8	24 1 50	13.1	14.4	.51	441			305.3	1.50	78
510	502	41 24.9	23 29 39	7.2	14.6	.00	5400	.25	30	278.5	26.62	170
520	518	41 28.2	23 36 20	7.6	10.6	—01	948	.37	473	268.5	6.21	54
524	522	41 28.5	24 20 57	8.9	11.5	—02	1805	.33	712	327.7	6.88	119
635	645	41 59.8	23 7 41	11.1	12.7	1.13	588	.28	344	114.1	26.07	105
641	640	42 7	24 25 48	13.9	14.1	.61	80	.49	56	359.9	13.56	121
644	649	42 1.4	22 53 1	10.8	14.5	1.35	359	.57	13	21.3	19.13	105
651	654	42 2.5	23 47 26	10.4	12.6	.31	1425			128.2	1.62	54
701	705	42 19.3	23 20 35	13.1	15.0	1.00	398	.82	35	28.8	20.05	105
778	776	42 45.1	24 1 25	12.1	15.7	1.14	941			280.8	17.55	162
790	799	42 48.7	22 52 59	13.7	14.9	.49	13	.44	1	48.3	17.96	245
796	791	42 49.3	24 48 48	13.5	15.4	.33	42	.40	1	236.2	8.97	246
819	821	42 56.4	24 14 18	13.1	15.3	.27	350			145.5	13.11	146
837	839	43 1.0	24 52 59	13.5	14.0	.99	42	.45	27	45.0	8.82	146
865	867	43 11.0	24 0 57	14.7	15.3	.37	8	1.46	2	35.1	6.70	53
870	881	43 12.8	23 44 53	3.6	14.8	—22	4944	.99	4	42.5	46.59	101
893	894	43 20.2	23 45 43	14.9	15.7	.35	11			130	5	53
999	1000	44 3	23 38 55	10.0	14.5	.21	841	1.13	16	182.3	8.93	144
1003	1002	44 1.5	23 32 41	6.8	10.9	—03	2401			239.9	3.54	221
1003	1001	44 1.5	23 32 41	6.8	10.9	—03	2401	.30	258	237.7	10.24	221
1003	998	44 1.5	23 32 41	6.8	15.4	—03	2401	.55	1	260	25	247
1040	1037	44 17.9	23 34 52	13.9	14.6	.23	70	.65	14	285.9	11.12	247
1066	1064	44 29.0	24 21 11	14.4	15.2	1.27	10	1.00	2	279.2	10.30	146
1175	1177	45 24.5	24 33 38	11.7	14.5	.81	78	.21	4	302.7	14.44	146
1189	1187	45 30.8	24 0 38	14.9	15.1					230.5	8.04	144
1192	1191	45 32.1	23 32 1	12.5	12.9	.22	80			299.2	1.69	144



The double star  $BD + 22^\circ 536$  found by TRÜMPLE (Publ. Astr. Soc. of the Pacific 33, 270; 1921) is just outside the field investigated in the present paper.

## 17. General Catalogue.

In the general catalogue given at the end of this paper all the results have been collected. It contains 1246 stars arranged according to their right ascension. Several objects, too faint for accurate determination of their effective wavelength have been included mainly to show the limit of the reliability of the results. For these faint stars the general catalogue has merely the character of a Durchmusterung.

The first column gives the current number of the star. In order to facilitate the identification of components of double stars, these have been marked: (comp. Table 15). Known double stars not recognized as such in the present paper have been marked with an asterisk \*. The next three columns give the star numbers according to WOLF (Ann. de l'obs. de Paris, Mém. Vol. 14, II, p. A 9; 1877), GAULTIER (Bull. de la Soc. astron. de France, Vol. 14, 445; 1900) and GRAFF (Astron. Abh. der Hamburger Sternw. zu Bergedorf, Bd. 2, Nr. 3; 1920). The fifth and the sixth columns give the right ascension and the declination for 1900, and the seventh column the number of plates on which the position is based. The eighth column gives the approximate photographic magnitude, which is only meant to serve for identification purposes, and the ninth column the number of plates used in evaluating the magnitude. The tenth and eleventh columns give the mean colour index  $I_\lambda$  and its weight, the mean error of  $I_\lambda$  being the square root of its reciprocal weight. In the twelfth column the colour index of SHAPLEY and RICHMOND (Contrib. from the Mount Wilson obs. No. 218, Ap. J. 54, 323; 1921), converted into the scale of  $I_\lambda$ , is given for comparison. The relation between  $I_\lambda$  and the colour index of SHAPLEY and RICHMOND was found to be as follows

$I, Sh \text{ and } R$	$\overset{m}{-}20$	0	20	40	60	80	1'00	1'20	1'40	1'60	1'80	2'00	2'20
$I_\lambda$ . . . . .	$-34$	$-12$	10	32	54	77	98	1'17	1'34	1'49	1'64	1'79	1'94

The weight of the  $I_\lambda$  values of SHAPLEY and RICHMOND is found to be  $20 m^{-2}$  corresponding to a mean error of  $\pm m \cdot 22$ . In deriving this mean error, systematic differences, which seem to be present between different regions of the field, have been disregarded. The most noticeable differences between the colour indices of SHAPLEY and RICHMOND and the effective wavelengths are shown by the stars no. 285 and 925. Especially for the fainter stars, where the weight of  $I_\lambda$  as derived from the effective wavelengths is small, the colour indices of SHAPLEY and RICHMOND form a welcome supplement. A comparison for the fainter stars of the two  $I_\lambda$  values in the tenth and the twelfth column tends to show, that the small weights of the  $I_\lambda$  values as derived from the effective wavelengths are somewhat greater than indic-

Table 16.  
Integrated weight of  $I_\lambda$ .

	plates from	measured at		number of stars	total weight of $I_\lambda$	fraction
effective wave- lengths	Mount Wilson	Potsdam	spectra of I order	1156	175116 $m^{-2}$	.471
			— - II —	57	25828	.070
			— - III —	92	44023	.118
				1169	244967	.659
	Copenhagen Urania Obs.	Copenhagen University Obs.		59	42071	.113
	all effective wavelengths			1169	287038	.772
colour- indices	Göttingen and Harvard, vis. Potsdam Pulkovo			19	5700	.015
				89	41407	.111
				234	24879	.067
	old colour indices			241	71986	.194
	total content of the 10 <sup>th</sup> column of the general catalogue			1169	359024	.966
	Shapley and Richmond, new colour indices			635	12700	.034
	grand total			1176	371724	1.000

ated. Thus the weights 4, 13, 22, 31 and 40 could accordingly be increased to 10, 20, 30, 40 and 50 respectively, but I have thought it safer to let them stand as they are.

The total weight of all the  $I_\lambda$  values of the general catalogue is 371724  $m^{-2}$ . This weight is distributed over the different series as indicated in Table 16.

It is seen that the Mount Wilson effective wavelengths contribute 66 percent of the total weight of  $I_\lambda$  and all the effective wavelengths together 77 percent, while the rest, 23 percent, is due to colour indices.

As is seen in the general catalogue the weight of  $I_\lambda$  is very different for different stars. Thus for 76 stars the weight of  $I_\lambda$  is greater than 1000  $m^{-2}$ . The total weight for these 76 stars is 214716  $m^{-2}$  or 58 percent of the weight for all the stars.

## 18. The Map.

The accompanying map of the Pleiades contained in the general catalogue was drawn to the scale of 1 second of time equal to 1 millimeter. It has been reduced to  $\frac{3}{10}$  of the original size. The scale is about 1 mm to 45''9, the equivalent focal length being 4494 mm.

The diameters of the dots representing the single stars increase with the apparent brightness of the stars in such a way, that a difference of 1 magnitude corresponds to a difference in the logarithmus of the diameter of .06. This is practically the same scale as used on the maps of the Bonner Durchmusterung.

On common photographs of stars the diameter of the images varies about  $1\frac{1}{2}$  times as rapidly with the magnitude but this would in the present case make the brightest stars inconveniently big if the faint stars are at the same time to be well visible.

The double and neighbouring stars contained in table 15 have been marked with a short line showing approximately the position angle of the pair. Special attention is called to the group of the 4 stars no<sup>s</sup> 1003, 1001, 1002, and 998, of which the three first named components are shown as one star on the map.

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I am greatly indebted to the director of the Mount Wilson Observatory, Professor GEORGE E. HALE, who not only immediately granted my request to use the 60-inch reflector for the determination of effective wavelengths, but also offered his assistance in realizing my plans. I owe the main part of the necessary funds and five months' leave from Potsdam to the Prussian government and the Academy of Science of Berlin. I wish also to express here my best thanks for the kind and disinterested help given to me by all of the Mount Wilson Observatory staff, not least to Mr. HOGE, the indefatigable night assistant.

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# General Catalogue.

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p=20$	Distance from Aleyone
				m s	° ' "		m		m	m-2		
1				36 40.0	24 0 41"	1	13.6	1	.			68
2				40.6	23 56 4	1	13.6	1	.27	18		67
3				41.9	23 34 2	1	11.9	1	.30	29		68
4				42.9	23 38 56	1	14.0	1	.18	4		67
5				49.8	23 57 5	1	10.5	1	1.01	22		65
6				49.9	23 45 4	1	12.9	1	.77	19		64
7				52.4	24 9 48	1	9.5	1	.26	3		68
8				58.5	24 10 29	1	8.1	1	.17	60		67
9				59.1	23 48 23	1	11.6	1	.24	26		62
10				37 3	23 33 25	1	10.2	1	.58	16		64
11				7.6	24 10 1	1	12.5	1	.82	24		64
12				17.1	23 51 24	1	13.2	1	.50	28	1.05	58
13	2		2	18.8	23 24 20	2	10.8	2	1.47	39		62
14			5	23.0	24 5 50	2	12.4	2	.41	76	.30	60
15			7	25.8	24 10 5	2	13.1	2	.59	33		61
16			8	25.9	23 42 49	2	13.7	2	.36	18	.48	56
17			9	28.9	24 18 4	1	13.8	1	.89	9	.99	63
18	4		10	34.8	24 20 7	1	12.7	1	.54	48	.40	63
19	6		11	36.6	23 21 29	1	10.8	1	.28	22	.26	60
20:	5		12	38.0	24 16 33	1	14.2	1	1.38	4	.57	61
21:				38.0	24 16 14	1	15.2	1	.89	1	.77	61
22	7		14	39.0	23 26 44	2	12.0	2	.60	87	.60	57
23				41.0	24 0 16	1	14.8	1	.23	4		54
24			17	42.2	24 25 25	1	14.2	1	.67	8	.13	65
25	9		18	42.8	23 13 13	1	10.5	1	.30	16		63
26				45.6	23 28 26	1	14.9	1	.12	2	.43	55
27	12		19	46.2	23 19 59	1	7.8	1	.11	36		58
28	11	1	20	46.6	24 3 28	2	8.1	9	.12	851		54
29	13		21	47.8	23 16 44	1	9.5	1	.01	52		60
30	14	2	24	52.1	23 43 19	2	11.5	6	.35	270	.68	50
31				53.5	24 16 38	1	15.2	1	.50	1		58
32	15	3	25	54.3	23 55 53	3	11.6	6	.40	200	.28	50
33	17		27	58.2	23 22 50	2	13.7	3	.63	32	.48	55
34	16	4	28	59.0	23 55 59	3	11.0	8	1.03	305	.98	49
35			30	59.2	23 23 36	2	14.8	2	.07	5		54
36		5	29	59.4	23 26 10	2	13.4	5	.41	89	.56	53
37	18	6	31	38 2	24 13 1	3	13.1	6	.81	219		55
38				6	24 11 38	1	15.6	1	1.20	2		54
39				1.4	23 58 1	1	14.2	1	.16	4		49
40	21		32	2.1	23 55 40	3	14.0	4	.54	39	.33	49
41	19	7	33	2.4	24 8 17	2	12.5	7	.33	323	.18	52
42				2.6	24 0 23	1	14.8	1	.41	4		50
43	20	8	34	3.1	24 14 31	2	8.1	11	.15	1121		55
44	23	9	35	3.2	23 34 1	2	9.8	11	.20	577		50
45	22	10	36	3.4	23 49 52	3	11.4	11	.98	418	1.24	48
46	24	11	37	4.1	23 53 10	3	12.3	9	.74	350	.40	48
47	26		38	5.7	23 13 41	2	10.9	2	.23	58	.21	58
48				6.2	24 40 20	1	10.2	1	.39	16		71
49	25	12	39	6.4	24 11 22	2	11.0	8	.35	408		53
50	27	13	40	7.0	23 55 41	3	13.2	7	.43	178	.22	48

## General Catalogue (continued.)

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p=20$	Distance from Alicorne
				m s	° ' "		m		m	m-2		
51	29		41	7.2	23 17 2''	2	13.1	3	.76	90	.70	56
52				7.2	23 48 54	2	14.5	5	.88	21	.48	47
53	30	14	42	7.6	23 52 20	3	13.2	7	.17	149	—22	47
54				8.2	23 45 27	1	14.7	2	.76	9	.40	47
55	28	15	43	8.3	23 57 35	3	12.2	8	.54	390	.23	48
56			44	8.3	24 25 55	2	13.9	2	.57	13	.62	60
57				8.4	24 41 10	1	13.6	1	.70	9	.64	71
58			45	8.6	24 4 49	3	14.7	3	1.75	16	1.32	50
59			46	9.3	24 1 39	2	13.9	4	.48	62	.44	48
60			47	9.8	24 1 13	2	14.0	4	.57	52	.53	48
61				10.2	23 51 34	2	14.5	4	.39	24		46
62	31		48	10.7	24 12 15	3	15.0	3	1.48	10		52
63	32	16	49	13.4	23 55 50	3	10.4	13	.27	551		46
64				13.5	23 27 51	1	15.3	1	—15	2		49
65	33		50	15.2	24 25 14	2	11.5	5	.25	227	.33	59
66				15.5	24 18 28	2	15.4	2	1.20	3		54
67	35	17	51	15.8	24 14 28	3	12.8	8	.27	238		52
68	34		52	16.2	24 27 48	2	10.6	2	.43	44		60
69	37	18	53	16.3	24 5 16	3	10.8	10	.33	532	.66	48
70			54	16.6	23 3 52	1	11.3	1	.44	44	.79	62
71	36	19	55	16.7	23 42 56	2	12.7	7	.79	220	.57	45
72				16.9	24 45 20	1	11.9	1	.65	58	1.07	73
73	38	20	57	17.1	23 42 53	2	12.1	8	.61	280	.52	45
74*	39	21	58	18.5	23 47 11	3	11.0	14	.47	539		44
75	41	22	59	20.0	23 57 23	3	11.0	13	.30	499		45
76			61	22.3	23 3 29	1	12.5	1	.69	24		62
77	42		60	22.3	24 28 48	2	10.8	2	.26	44	.22	60
78	40		62	22.3	24 33 28	2	9.9	2	1.41	12		63
79				22.5	24 14 34	2	14.5	4	—41	24		51
80	43		63	22.8	24 27 26	2	11.5	6	.64	168	.91	59
81	44	23	64	22.9	23 56 42	3	12.5	10	.34	463	—06	44
82			65	24.2	24 27 8	2	14.4	4	.96	8	.84	58
83	46		66	25.5	23 39 19	2	13.7	5	.86	57		43
84	45		67	25.8	23 12 8	2	13.7	2	.83	18	1.05	55
85				26.0	24 20 6	1	15.6	1	.81	2		53
86				26.9	23 35 42	2	14.6	2	.54	8		44
87				27.1	23 45 13	1	14.9	1				42
88	47	24	68	27.3	23 49 4	3	9.3	22	.22	1525		42
89				27.5	23 17 47	1	14.9	1	.57	2		52
90	48	25	69	27.5	24 6 34	2	13.7	6	1.20	108	1.33	46
91	50	26	70	28.5	23 21 10	3	12.0	8	1.02	388	.82	50
92	51	27	71	28.7	24 4 46	2	8.4	15	.14	1717		45
93	49	28	72	28.9	24 16 28	3	12.5	8	.67	380		51
94				30.2	23 54 19	1	15.3	1	1.56	1		42
95				30.6	23 53 0	2	15.0	2	.77	1		42
96				31.6	23 51 23	2	14.7	7	.82	26		41
97			73	32.1	24 23 55	2	14.1	5	.47	38	.29	55
98				37.5	23 53 48	1	15.6	1	1.10	2		40
99	54		74	38.5	23 22 27	2	13.6	5	.81	87	.81	47
100				38.7	24 19 23	1	15.2	1	.75	2		51

## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$mpg$	Number of images	$I_\lambda$	$p$	$I_\lambda$ Sh. and R. $p = 20$	Distance from Alycone
				m s	$24^\circ 43' 21''$	1	m	1	m	m-2		
101				38.7	24 43 21	1	14.0	1	.57	8	.42	68
102				38.9	24 49 16	1	15.0	1	1.59	1		73
103	53	29	75	39.2	23 44 49	3	13.3	11	1.55	267	1.64	40
104	58		76	39.2	23 24 29	3	13.9	6	.76	51	.51	46
105				39.3	24 38 47	1	14.6	1	.80	4	.67	64
106				40.0	24 0 11	2	14.7	5	.66	22		41
107	57	30	77	42.2	24 11 44	3	11.5	10	.37	428	.72	46
108	56		78	43.0	24 30 12	1	10.0	7	.17	217		57
109	59	31	79	44.7	24 4 58	3	12.4	9	.51	404	.57	42
110				45.0	22 58 24	1	13.6	1	.06	9		62
111			80	45.2	23 58 14	3	13.7	10	.30	174	.49	40
112				45.8	24 17 35	1	15.2	1	1.74	2		48
113				46.3	24 44 38	1	13.6	1	.46	18	.52	68
114				46.6	23 24 5	1	14.9	1	1.77	4		44
115	60	32	82	47.4	23 54 59	3	12.1	16	.66	576	.59	38
116	61	33	83	48.7	24 24 53	2	13.4	6	.80	168	1.25	53
117	62	34	84	51.5	23 58 30	3	5.5	31	—18	4536		38
118	63	35	85	52.7	23 50 52	3	13.1	11	1.60	305	1.62	37
119	64	36	86	52.9	23 44 22	3	13.0	12	.54	344		37
120				52.9	24 34 22	2	14.2	2	.38	13	.57	59
121				53.2	24 6 7	2	14.7	2	.34	8	.81	41
122	65	37	87	53.4	23 16 30	2	11.1	9	1.34	414		48
123				54.7	22 57 17	1	8.4	1	.05	65		62
124				55.0	23 4 33	1	13.6	1	.50	18	.71	56
125				55.8	24 37 38	2	14.4	2	.24	8	.58	61
126	66	38	88	56.2	23 47 56	3	3.6		—21	4391		36
127			89	57.2	24 24 54	2	14.2	5	.65	42	.89	51
128				57.9	24 4 46	1	15.2	1	1.28	1		39
129	68	39	90	58.0	23 36 25	3	11.3	11	.48	410	.67	37
130				58.8	24 29 21	1	15.2	1	.77	1		54
131	67	40	91	58.9	24 28 20	2	13.2	7	1.08	197	1.10	54
132				59.3	23 17 41	1	14.3	1	1.05	4		46
133	69	41	92	59.3	24 7 7	3	10.9	11	.39	457	.54	40
134			93	59.9	23 3 17	1	13.6	1	.56	18	.59	56
135			39	.7	23 46 32	1	14.6	2	1.34	4	1.28	35
136				2.0	24 20 25	1	15.6	1	.56	2		47
137				2.4	23 38 1	2	14.8	2	.74	10	1.09	36
138	70	42	94	3.6	24 16 11	3	13.5	7	1.48	134	1.64	44
139				5.3	23 46 37	3	14.0	7	.08	61	.50	34
140				6.3	24 14 38	1	15.2	1	—31	1		43
141	71	43	96	7.6	23 31 32	3	12.6	8	.80	331	1.26	37
142				8.4	24 40 17	1	14.6	1	.34	2	.76	62
143	78		97	8.5	23 4 50	1	13.6	1	.57	18	.47	54
144				9.1	24 42 57	1	12.2	1	—11	56	.32	64
145	73	45	99	9.9	23 23 19	3	9.2	17	.11	1223		41
146	72	44	98	9.9	23 56 57	3	8.9	29	.16	1766		34
147				10.5	24 27 23	2	13.8	6	.35	80	.28	51
148				11.0	23 22 10	1	14.9	1	.63	2		41
149				11.1	24 21 39	2	14.1	4	.62	42	.48	47
150	76	46	100	11.8	24 31 29	2	5.7	12	—21	3263		54



## General Catalogue (continued).

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p=20$	Distance from Aleyone
151	77	47	101	m s 12.8	24° 10' 12"	3	m 11.4	10	m -43	m-2 452	-36	39
152				39 13.5	23 56 50	4	15.0	4	.71	9		33
153				14.3	24 11 44	1	15.2	1	.83	1		40
154				14.6	24 16 20	2	15.2	2	.73	6		42
155				14.7	24 56 23	1	13.2	1	.27	14		75
156	79	49	103	15.2	24 9 11	3	4.2		—22	3701		38
157	80	48	102	15.2	23 34 50	3	13.1	7	.68	155	.90	34
158	82	50	104	16.2	23 48 37	3	12.9	13	.96	441	1.23	31
159	75		105	17.2	24 37 8	2	12.8	2	.42	86	.57	58
160				17.5	22 45 46	1	12.2	1	1.20	56		69
161				17.6	23 31 54	1	15.3	1	.74	2		35
162				18.1	22 58 53	1	12.5	1	.16	48	.82	57
163				18.6	24 9 40	2	15.4	2	1.06	1	1.35	38
164	81		106	19.3	24 34 26	2	12.3	4	.19	174	.30	56
165				19.4	22 48 37	1	9.0	1	.75	63		66
166	83	51	107	19.9	24 24 34	2	12.1	8	.37	368	.28	48
167				22.1	24 33 26	2	14.2	4	.11	46	.42	54
168	85		109	22.7	23 50 19	3	13.7	11	.28	165	.42	30
169	84		108	22.8	24 36 28	2	8.6	2	.21	132		57
170	86	52	110	23.1	23 51 56	3	11.0	21	.26	775	.31	30
171				23.5	24 18 23	2	14.3	5	.40	38	.60	42
172	88		111	24.1	23 47 35	2	14.4	6	.54	47	.67	29
173				24.1	24 9 25	1	15.2	1	1.15	1		36
174				25.3	23 56 13	1	15.2	1				30
175	89		112	25.7	23 24 50	3	13.5	7	.69	132	.66	37
176	87	53	113	25.9	24 34 22	3	9.8	9	.19	455		55
177				26.3	24 25 4	4	15.4	4	.78	4		47
178				26.5	24 1 49	3	14.7	3	.62	14		32
179				26.7	23 22 17	2	15.1	2	.57	6		38
180				27.3	24 24 44	2	14.6	5	.99	18		47
181	93	54	114	27.3	23 9 29	2	13.3	6	.82	136	.62	47
182				28.5	22 53 28	1	8.2	1	.41	60		61
183				29.0	23 47 58	1	14.3	1				28
184	92		115	29.3	23 45 20	2	14.0	8	.49	70	.53	28
185	94	55	118	29.6	23 10 19	2	12.7	6	.49	266	.62	47
186			116	29.6	24 12 35	3	14.7	4	.49	18	.76	37
187	91	56	117	29.9	23 43 19	3	8.3	33	.13	2573		28
188				29.9	24 11 22	1	15.2	1	.39	1		37
189	90		119	30.5	24 17 59	3	14.6	5	1.03	26	.68	41
190				30.9	24 53 37	1	14.0	1	.34	4		71
191				31.1	22 52 45	1	10.5	1	.82	22		61
192	95	57	120	31.2	23 7 1	2	13.0	7	.51	205	.79	49
193	97		121	32.5	23 55 52	3	13.9	9	1.50	107	1.38	29
194				32.9	22 48 3	2	12.5	1	.62	48	.92	65
195				32.9	22 56 35	1	13.6	1	1.02	18	.97	58
196	98	58	122	33.2	23 5 8	2	12.8	5	.28	190	.59	50
197				34.2	23 26 52	2	14.9	3	1.29	11	1.19	34
198				35.1	24 42 8	1	14.0	1	1.10	8	.64	60
199				35.6	24 15 23	1	15.8	1				38
200	99		123	35.9	23 33 23	3	13.5	7	.46	123	1.04	30

## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_k$	$p$	$I_k$ Sh. and R. $p = 20$	Distance from Aleyone
				m s	° ' "		m		m	m <sup>2</sup>		'
201	104		124	36.1	23 18 25	2	13.6	6	.57	124	.77	39
202				36.1	23 59 24	3	14.1	10	1.14	58	.94	29
203				36.1	24 52 28	1	13.6	1	1.76	9		70
204				36.5	23 58 10	3	15.4	3	1.42	4		28
205				36.8	24 50 17	1	13.6	1	.06	18		68
206	101	59	125	39 37.2	24 9 2	3	9.0	22	.17	1624		34
207				38.0	22 57 14	1	14.0	1	.71	4	.52	57
208				38.0	24 15 30	2	15.4	2	1.20	4		38
209				38.1	24 6 13	1	15.2	1	.76	2		32
210	100	60	126	38.5	24 35 16	2	11.6	9	1.10	405	1.05	54
211	102	61	127	38.7	24 11 10	3	12.6	13	.32	509	.41	35
212			128	38.9	23 36 46	3	13.8	9	.31	131	.59	28
213	103	62	129	39.1	23 46 13	3	10.5	27	.30	1147		26
214				39.7	23 2 32	2	14.6	2	.73	12	.74	52
215				40.6	23 57 0	3	14.5	9	.88	38		27
216	105	63	130	40.8	24 1 23	4	7.4	36	.04	3764		29
217				41.3	22 46 56	1	12.5	1	.40	48		66
218			131	41.3	23 35 58	3	14.0	8	.79	75	.80	28
219	107	64	132	42.6	24 18 50	2	10.1	21	.24	1086		40
220				43.1	22 44 16	1	12.9	1	.49	19		68
221:			134	43.5	24 8 41	3	13.9	8	.23	71		33
222				43.7	24 36 17	3	14.3	4	.21	27	.58	54
223	108		133	43.8	23 26 29	3	13.3	8	.80	204	1.16	33
224:				43.8	24 8 40	2	14.9	2	.39	6		32
225	106	65	135	43.8	24 35 34	3	9.9	12	.29	402		54
226				44.0	24 44 35	2	14.0	2	1.04	26	1.05	62
227	109	66	136	44.5	23 58 33	3	9.9	31	.23	1556		27
228	110	67	137	44.6	24 7 7	3	11.9	16	.56	642	.79	31
229				45.0	22 44 40	1	12.2	1	.04	56		67
230	113	68	138	46.6	23 57 25	3	12.4	21	.48	744	.63	26
231				46.8	24 22 8	2	15.4	2	.18	4		42
232	112	69	139	46.8	24 24 0	3	12.7	13	1.63	516	1.38	44
233				47.1	24 40 24	3	12.8	3	.96	130	.83	58
234	114	70	140	47.7	23 54 28	3	11.0	27	.43	927	.41	25
235				49.3	23 15 58	1	16.1	1				39
236				49.6	23 38 59	3	14.8	4	.06	17		25
237	111		141	50.5	24 33 53	3	13.5	8	.41	158	.59	52
238				50.7	24 8 10	3	15.1	4	.48	11		31
239				51.1	23 16 19	1	15.6	1				39
240	118		142	51.3	23 17 14	3	13.8	8	.49	130		38
241	116	72	144	52.4	24 6 49	3	12.0	18	1.16	414	1.16	30
242	115	71	143	52.4	24 3 19	4	3.8		.20	4612		28
243				52.8	23 47 22	1	14.9	1	.47	4		23
244				53.0	23 33 21	2	14.4	2	.99	16		27
245				53.1	23 38 6	3	14.7	4	.37	20		25
246				53.2	23 32 23	1	15.3	1	1.06	1		27
247				53.4	24 17 17	3	15.0	3	.75	12		37
248*				54.6	22 50 5	2	5.8	2	.15	305		61
249				54.8	23 33 41	2	15.2	2	1.38	6		26
250				55.1	23 2 7	2	14.8	2	1.26	8		50

## General Catalogue (continued.)

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p = 20$	Distance from Alcyone
				m s	$^{\circ} \quad ' \quad ''$		m		m	$m^{-2}$		'
251	120	73	145	40 55.3	23 43 36	4	8.2	48	.13	3107		22
252	122		146	55.4	23 18 28	3	13.4	8	1.00	206	1.12	37
253	117	74	147	56.4	24 29 18	3	12.9	12	.58	352	.63	47
254	125	75	148	56.7	23 7 8	3	12.7	9	.48	371	.14	46
255	121	76	149	57.1	24 14 30	2	5.9	30	—13	4608		34
256	123		150	57.9	23 56 22	4	13.8	15	1.55	192	.167	23
257	128		151	59.7	23 8 41	1	15.1	1	1.06	4	1.17	44
258				40 .1	22 49 48	2	13.1	2	.34	52	.99	61
259				.5	24 3 48	4	14.0	13	.58	117	.56	26
260				.8	24 44 19	2	9.7	2	.12	96		60
261				.9	24 42 46	1	15.0	1	.86	2		59
262				1.8	24 12 49	1	15.2	1	.20	2	.77	32
263	124	77	152	3.9	24 31 32	3	12.7	12	.23	470	.43	48
264				4.1	24 6 35	4	14.1	10	.18	88	.61	28
265	129	78	153	5.4	24 12 53	2	6.7	32	—11	4631		32
266				5.9	24 53 42	2	13.1	2	.37	57		69
267				6.9	23 35 4	3	14.4	4	.56	24		23
268	132		154	7.2	23 25 31	3	13.7	8	.86	132		29
269				7.4	24 40 47	2	10.3	10	.08	379	.59	56
270	131	79	156	7.7	23 43 58	4	12.5	20	1.12	766		20
271				7.8	24 42 17	2	10.9	6	.27	160	.01	58
272	130		155	8.0	24 26 4	2	14.6	5	.96	28	1.22	43
273	133		158	8.9	24 15 17	3	13.9	9	1.06	124	1.35	33
274				8.9	24 49 47	2	12.2	2	.26	114		65
275			157	8.9	24 34 16	3	14.5	7	.46	39	.87	50
276		80	159	9.1	24 31 40	3	13.5	10	.06	216	.74	48
277	135		160	9.3	23 5 37	2	13.6	5	.84	116		46
278				9.3	24 15 1	3	14.9	8	1.40	21	1.16	33
279	127	81	161	9.4	24 33 16	2	12.9	10	.82	339	.70	49
280				9.4	22 59 47	2	14.4	3	1.46	18	.98	51
281				9.8	22 47 50	2	13.9	2	.56	13		63
282				10.6	24 0 2	4	14.9	5	.36	15		22
283				10.7	23 49 44	1	15.3	1				19
284				10.7	24 18 53	1	15.8	1				36
285				10.9	24 36 18	3	14.0	5	.19	62	1.10	52
286				10.9	24 37 7	3	13.8	5	.32	72	.47	53
287	134		163	11.4	24 19 19	3	14.2	9	.76	78	.69	37
288	126		162	11.4	24 35 47	2	15.1	5	1.07	14	1.06	57
289	137	82	164	11.6	23 44 54	3	10.9	30	.32	1046		19
290				11.7	22 54 22	2	10.8	3	1.33	48		56
291				12.0	23 54 48	1	15.9	1				20
292				12.7	23 45 43	2	15.2	2	1.51	6		18
293				12.9	22 49 16	2	12.7	2	1.56	86	1.48	61
294				13.3	23 2 10	1	15.1	1	2.64	4		49
295	138	83	165	14.0	24 18 38	3	12.5	16	.69	552	.66	36
296				14.7	23 44 50	2	14.8	9	.58	34		18
297				14.9	22 59 24	1	15.0	2	1.16	6	1.15	51
298		84	166	15.3	23 1 41	2	10.2	10	.35	453		49
299				15.6	22 49 25	2	13.9	2	.47	22		61
300				16.4	23 44 34	3	15.8	3				18



## General Catalogue (continued.)

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$mpg$	Number of images	$I_k$	$p$	$I_k$ Sh. and R. $p = 20$	Distance from Aleyone
				<sup>m s</sup> 40 16.4	<sup>° ' "</sup> 24 43 45	2	<sup>m</sup> 13.7	4	<sup>m</sup> 19	<sup>m-2</sup> 83	.66	59
301				16.8	23 2 18	1	15.6	1				48
302				16.9	23 15 52	1	14.6	1	.34	8		36
303				16.9	24 5 10	3	15.0	4	1.11	13		25
304				17.0	23 53 3	4	9.1	41	1.17	2183		18
305:	141	85	167									
306:			168	17.1	23 53 22	2	13.8	6	.32	92	.60	18
307				17.5	24 18 44	3	15.1	3	.91	10	1.24	35
308				17.8	24 45 1	2	14.4	3	.17	30	.58	60
309				17.8	22 53 50	2	14.9	3	1.21	10	.86	56
310				18.3	22 49 1	2	8.3	2	.44	120		61
311				18.8	24 28 7	3	15.3	4	.34	8		44
312	142		169	19.2	23 40 22	4	13.7	15	.65	235	.56	18
313*	143	86	170	19.3	23 52 42	4	8.4	46	.14	3014		17
314				19.7	24 57 30	2	14.0	2	1.38	9		72
315				20.1	24 49 56	2	14.7	2	.61	9		64
316	139	88	172	20.7	24 30 34	3	13.2	11	.36	266	.31	46
317	140	87	171	21.0	24 33 28	3	12.7	13	1.03	487	.61	48
318				21.1	23 36 28	3	15.2	3	1.14	2		20
319	145		173	21.8	24 1 14	4	14.5	6	1.08	35	.69	21
320				22.1	23 58 5	3	15.4	3	.36	6		19
321				22.2	24 28 26	1	15.4	1	.50	1		44
322	147	89	174	22.9	23 10 31	3	11.0	16	.44	724	.60	40
323	146	90	176	23.4	23 38 14	4	4.2		.19	5154		18
324	144		177	23.5	23 43 25	3	13.4	12	.20	176	.21	16
325				23.6	23 36 20	3	15.0	3	.65	12	.44	19
326			175	23.9	23 41 46	2	14.6	9	.45	52		17
327	149	91	178	24.4	23 12 32	3	13.1	10	.65	253	.72	38
328				25.0	24 54 2	2	10.3	2	.76	42		68
329	148	92	179	25.0	24 15 29	3	11.0	23	.37	845	.28	32
330				25.0	24 38 22	3	14.4	6	.06	20		53
331				25.9	22 41 51	1	13.0	1	.35	19		67
332	150		180	27.0	24 2 59	4	13.6	16	.93	250	.67	21
333				27.2	24 42 20	2	12.1	6	1.54	296	1.50	56
334				27.5	24 38 8	3	13.5	6	.26	130	.32	52
335				27.5	23 2 8	1	15.6	1				48
336				28.4	24 49 26	2	10.6	2	.27	32		63
337		93		29.6	23 0 40	2	11.3	9	.95	338	1.17	49
338				29.8	23 43 8	3	15.1	3	.91	8		15
339				29.9	23 38 5	1	14.9	1	.48	4		17
340				30.0	24 53 46	1	15.0	1	.44	2		67
341	151	94	181	30.3	23 56 40	4	7.6	65	.08	5107		17
342				30.9	24 55 0	2	13.8	2	.66	32		69
343	152	95	182	31.1	24 7 22	3	11.8	24	.49	964	.24	24
344				31.5	23 34 34	3	14.4	7	.55	56		19
345				31.8	25 0 44	1	10.6	1	.18	16		74
346	156		183	32.3	23 16 53	3	13.7	7	.93	136	.88	34
347			184	32.6	24 3 41	4	14.5	6	.69	32		21
348			185	32.9	23 3 47	2	14.1	4	.43	44	.53	46
349				33.0	23 39 37	3	15.4	3	.87	4		16
350			186	33.4	23 54 35	4	14.6	5	.46	27		15

## General Catalogue (continued.)

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p=20$	Distance from Aleyone
351				m s 40 33.5	24° 44' 47"	2	m 13.7	4	m -79	m <sup>-2</sup> 82		58
352				33.6	23 34 19	3	15.0	6	-45	8		19
353			187	33.8	23 4 4	2	14.6	4	-65	21	-63	45
354	154	96	188	34.0	24 33 30	3	10.0	22	-16	874		48
355				34.5	22 47 49	1	13.6	1	-83	9	-48	61
356				34.7	23 48 21	1	15.3	1				13
357	155		189	34.7	24 1 18	3	13.9	14	-29	171	-17	19
358			190	34.9	24 0 41	3	14.2	12	-39	106	-18	18
359				35.5	23 58 10	1	14.9	1	-35	4	-88	17
360	157		191	35.6	23 40 21	2	14.7	8	1.10	33	1.01	15
361				35.6	22 52 19	2	11.8	3	-50	154	-49	57
362	158	97	192	36.1	23 33 2	3	11.4	28	-41	968	-03	19
363				36.5	24 16 33	3	14.6	8	-39	50	-33	31
364				37.3	24 25 53	1	15.7	2	1.41	2		40
365	159	98	193	37.3	23 49 40	4	12.7	31	-56	946	-23	13
366	164		194	37.5	23 32 7	3	13.6	15	1.20	291	1.05	20
367				37.8	24 52 26	2	13.6	2	-08	37		66
368	163	100	196	38.6	23 39 3	3	12.0	31	-30	931	-19	15
369	162		197	38.7	23 40 44	3	13.7	7	-85	103	-57	14
370				38.7	24 27 30	2	14.2	6	-33	59	-01	42
371	161	99	195	38.7	23 18 47	3	8.5	30	-20	2244		31
372	165		198	38.8	23 29 19	4	13.6	12	-35	241	-52	22
373				39.6	23 39 19	2	15.5	3	-74	3		15
374	160	101	199	39.7	24 26 13	3	12.8	14	-85	402	-46	40
375				40.0	24 8 53	2	15.5	1	-30	4		24
376		102		40.2	24 38 56	2	10.7	10	-28	398	-64	52
377				40.2	24 46 49	1	15.4	1	-55	2		60
378	166		200	40.2	24 1 57	3	13.3	20	-99	403	-67	19
379				40.3	24 37 56	2	14.4	4	-94	24	1.06	51
380				41.3	24 12 33	3	14.6	6	1.19	32	-94	27
381				41.6	23 32 16	3	14.9	3	-72	14		19
382				41.7	24 53 55	1	14.5	1	-28	4		67
383	167		202	41.7	24 30 28	3	13.7	11	-66	156	-56	44
384				41.7	23 52 44	1	15.3	1	-02	2		13
385	168	103	201	41.8	23 28 36	4	10.6	31	-52	1225		22
386				42.0	24 35 27	2	14.2	4	-64	38	-44	49
387	170		203	42.2	23 40 59	3	14.0	16	1.39	179	-93	13
388	169	104	204	42.7	23 47 34	2	9.6	42	-21	2055		11
389	171		205	42.9	24 2 25	3	14.0	15	-63	153	-17	19
390	172	105	206	42.9	23 43 8	2	13.1	20	-84	513	-36	12
391				43.2	24 54 42	2	13.6	2	-01	37		68
392				44.1	23 44 59	1	15.3	1	-30	2		11
393				44.3	23 25 59	1	15.1	1	-92	4		24
394				44.8	25 2 45	1	12.9	1	-18	48		76
395	173		207	45.2	23 11 11	2	13.1	9	-78	236	-46	38
396				45.8	22 48 0	2	8.8	2	-04	133		60
397				46.0	23 38 25	3	15.1	3	-89	8		14
398				46.0	23 57 59	1	15.3	1	-26	2		15
399				46.1	24 58 57	1	13.6	1	-13	28		72
400				46.5	24 37 8	2	13.9	5	-61	72	-58	50

## General Catalogue (continued.)

No.	Wolf	Gould	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_k$	$p$	$I_k$ Sh. and R. $p = 20$	Distance from Aleyone
				m s	° ' "		m		m	m <sup>-2</sup>		
401:	174		208	40 46.7	23 56' 41"	2	14.2	11	.55		.76	14'
402:				46.8	23 56 40	1	15.3	1				14
403	175	106	209	47.3	24 0 5	2	10.8	37	.19	1312	.19	16
404				47.4	23 1 47	2	14.2	4	.19	28	.21	47
405				47.5	24 19 0	3	14.3	9	.53	66	.08	33
406				47.6	23 42 37	1	14.9	1				11
407:				48.7	24 1 51	1	14.4	1				17
408:	176	107	210	48.8	24 1 50	3	13.1	19	.51	441		17
409			211	48.9	24 17 31	3	14.9	5	.69	20	.70	31
410				49.3	24 35 17	2	14.4	4	.52	24	.49	48
411	178		212	49.5	23 30 52	3	13.7	14	.36	271	.23	19
412				50.3	24 54 42	2	13.2	2	.21	52		68
413	177		213	50.7	24 14 52	3	13.5	15	.42	260	.09	29
414				51.6	23 30 49	4	15.0	8	.95	16		19
415				52.3	22 50 32	2	12.4	3	.98	168	.87	58
416				53.2	24 48 55	2	10.6	9	.18	167		62
417				54.0	24 54 50	2	12.9	2	.66	86		68
418				54.5	24 39 12	2	13.9	5	.65	73	.33	52
419			214	55.7	23 51 43	4	14.5	6	.62	47	.47	9
420		108		55.9	22 55 43	2	9.9	10	.21	475		52
421				56.0	23 40 56	4	15.2	6	.31	20		11
422				56.1	24 49 56	1	15.0	1	1.14	2		63
423				56.3	23 51 25	2	15.6	3	1.40	2		9
424	179	110	216	56.4	24 29 10	3	10.9	19	.39	723		42
425	180	109	215	56.6	24 36 38	2	11.7	9	.40	407	.67	49
426				57.6	23 48 2	1	15.3	1	1.77	2		8
427		111		57.8	22 53 58	2	10.7	9	.85	282	.98	54
428	181	112	217	58.3	23 16 22	3	10.9	23	.37	862	.12	32
429				58.4	23 25 41	1	14.8	2	1.49	8		23
430			41	.1	23 50 16	2	15.1	3	1.51	5		8
431				.2	24 10 30	2	15.3	3	.50	3	.86	24
432	185		218	.4	23 30 24	4	13.7	12	.49	215	.44	19
433				1.3	24 46 49	2	13.9	4	1.55	54	1.25	59
434				1.6	22 59 51	2	14.2	4	1.08	25	.72	48
435				1.7	24 51 8	1	14.4	7	.50	4		64
436	182	113	219	1.8	24 12 34	4	7.0	57	.05	5655		26
437	184	114	220	2.2	23 46 40	2	12.7	26	.34	794	.26	7
438				2.4	23 2 16	2	15.1	2	1.13	5		46
439				2.5	23 2 58	1	15.5	1				45
440	186	115	221	2.5	24 4 25	3	11.1	33	.28	1177	.32	18
441				2.6	23 26 53	1	15.5	1	.27	2		22
442	183	116	222	2.8	24 1 14	2	12.7	26	1.10	759	1.31	15
443				3.2	22 46 56	2	13.6	2	.76	27		61
444	187	117	223	3.9	23 40 20	2	12.9	23	.86	717	.82	10
445				4.0	23 26 11	3	15.0	4	.40	14		22
446	190		224	4.2	24 3 44	3	14.8	6	1.15	24		17
447*	188	118	225	5.1	24 30 36	3	8.8	26	.19	2089		43
448				5.5	23 33 50	3	14.3	3	.27	30	.10	15
449	189	119	226	5.8	24 19 35	3	11.7	25	1.22	940	1.71	32
450				5.8	23 50 20	3	14.9	4	.22	16		7



## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_k$	$p$	$I_k$ Sh. and R. $p = 20$	Distance from Aleyone
				m s	° ' "		m		m	m-2		
451	191	120	227	41 6.0	24 53 58	2	12.5	2	.21	104		66
452				6.2	23 11 7	2	12.1	12	.62	463	.94	37
453				6.7	22 57 32	2	14.0	4	.25	26	.66	50
454				7.0	23 50 58	1	15.1	1				7
455				7.0	23 23 49	3	14.8	5	.68	20	.23	24
456	192	121	228	7.1	22 49 36	2	13.9	3	.69	35	.52	58
457				7.7	23 41 7	2	8.6	64	.15	3466		9
458				9.8	23 24 30	2	15.6	2				24
459	193	122	229	10.1	24 33 39	3	12.9	8	.45	307	.31	46
460			230	10.5	23 7 29	2	14.1	4	.11	48	.37	40
461	194		231	10.8	24 12 55	3	14.3	10	1.19	94	1.05	26
462	197		232	11.1	23 24 19	4	13.2	17	.93	388	.50	24
463				11.3	23 28 26	1	15.5	1	1.07	2		20
464				11.3	23 15 39	1	15.1	1	1.10	4		32
465			233	11.9	23 10 15	2	14.0	4	.30	43	.33	37
466				12.6	22 55 2	1	14.6	1	2.32	8		53
467	196	123	234	12.8	23 24 2	3	15.2	7	1.06	10	1.08	24
468				13.0	23 58 1	2	9.6	55	.17	2391		11
469				13.1	24 46 19	1	15.0	1	.07	4	.73	59
470				13.2	24 7 32	3	14.4	7	.48	56	.50	20
471				13.2	24 48 32	2	11.5	8	.21	244	.21	61
472	198	124	235	13.3	23 2 46	1	15.5	1	.12	2		45
473				13.4	23 56 46	1	15.3	1	1.39	2		10
474				14.0	25 2 46	1	12.3	1	.02	58		75
475				14.2	23 28 17	4	9.8	45	.28	2041		20
476				14.3	23 44 2	4	14.8	8	.35	30	.26	5
477	195		236	14.4	23 53 41	4	14.3	8	.31	59	.26	7
478				15.2	25 3 41	1	11.1	1	.08	28		76
479				16.0	24 29 25	2	15.4	3	.00	6	.73	42
480				17.1	24 58 56	1	9.9	1	1.06	48		71
481				17.9	23 24 16	4	13.6	17	1.07	277	.63	24
482	206		238	18.0	23 48 29	3	14.0	8	.39	72	.41	3
483	199	125	239	18.3	23 52 56	1	13.0	23	.33	549	.53	6
484	202	126	240	19.7	23 49 5	1	9.1	63	.23	2891		3
485	204	127	241	20.4	23 30 28	4	11.5	29	.64	1016	.80	17
486	207	128	242	20.5	23 15 45	1	14.6	1	.32	8		32
487				20.7	24 4 55	3	14.0	11	1.26	158	.83	17
488				20.9	23 36 13	3	12.4	24	1.33	883	1.35	12
489				21.0	24 50 0	2	12.5	6	.36	253		62
490				21.2	23 47 25	2	15.2	4	1.12	9	.80	3
491	205	129	244	21.2	24 8 37	4	12.7	24	1.01	748	1.04	21
492	201		245	21.4	24 20 0	4	14.0	12	.31	123	.16	32
493	208	130	246	21.6	23 43 38	2	15.2	3	.73	8		5
494				21.7	23 25 0	5	7.5	61	.30	4481		23
495				21.9	22 56 29	2	14.2	4	.12	28	.67	51
496	203	131	247	22.2	23 17 10	2	15.2	2	.70	5		30
497				22.2	22 36 52	1	11.7	1	.81	52		71
498				22.5	24 33 51	3	13.1	7	.36	210	.63	46
499				22.5	24 13 11	2	15.3	2	.61	6		26
500				22.6	23 38 27	3	14.8	5	.34	24	.57	9

## General Catalogue (continued.)

No.	Wolf	Gaullier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_k$	$p$	$I_k$ Sh. and R. $p=20$	Distance from Alcyone
				m s	$^{\circ}$ $'$ $''$		m		m	m-2		'
501	209	132	248	41 22.6	23 49 49	3	8.5	73	-14	3913		3
502:				23.0	23 29 41	3	14.6	9	-25	30		18
503	211		249	23.2	23 41 31	4	14.1	11	-90	140	-68	7
504				23.6	24 39 40	1	14.9	2	-60	6	-71	52
505				24.0	24 51 49	1	14.0	1	-20	18		64
506				24.2	23 0 10	2	13.9	4	1.35	53		47
507			251	24.3	23 46 14	5	13.9	15	1.01	123	-69	2
508	212	133	250	24.4	23 48 26	3	6.4	85	—02	6263		2
509				24.5	24 50 11	1	15.4	1	-63	2		62
510:	213	134	252	24.9	23 29 39	4	7.2	60	—00	5400		18
511				25.4	23 42 28	2	14.7	3	1.35	16		5
512				26.2	24 44 36	2	14.3	4	1.33	25	1.13	57
513	214	135	253	26.2	24 16 45	5	7.9	60	-12	4099		29
514				26.2	23 21 13	1	15.5	1	1.06	2		26
515				26.6	24 23 19	1	14.9	2	1.53	8		35
516				27.4	24 5 5	1	15.0	2	1.03	7		17
517	215	136	254	27.5	23 14 41	4	11.2	20	-27	680	-14	33
518:	216		255	27.6	23 36 19	2	10.6	34	-37	473		11
519				28.1	23 46 52	1	14.6	7	1.11	12	1.38	1
520:	217	137	256	28.2	23 36 20	2	7.6	57	—01	948		11
521				28.2	24 26 58	2	14.8	5	—07	24		39
522:	218	138	257	28.3	24 21 2	4	11.5	26	-33	712	-08	33
523				28.5	23 35 16	3	14.9	5	-75	19	-78	12
524:	219	139	258	28.5	24 20 57	4	8.9	41	—02	1805		33
525				28.8	24 3 17	1	14.3	1	1.02	8		16
526				28.9	22 36 47	1	7.4	1	-06	62		71
527				29.1	23 44 29	1	14.9	1	-41	4		3
528	221		259	29.4	24 11 53	4	13.6	18	-29	283	-41	24
529	223		260	29.9	23 19 15	4	13.6	1	1.01	238	1.21	28
530				30.3	23 55 1	1	15.3	1	2.00	2		7
531	224	140	261	30.5	23 13 56	4	11.8	17	1.08	620	1.19	34
532				30.6	24 25 4	1	15.4	1	-53	2		37
533				30.8	24 9 17	1	15.2	2	-45	6		22
534	225	141	262	31.1	23 22 8	5	7.9	58	-10	4049		25
535	222	142	263	31.2	24 14 47	5	12.5	26	1.56	931	1.56	27
536				31.3	23 26 18	2	14.8	4	-91	22		21
537				31.6	23 34 19	3	15.0	4	-33	18		13
538	220	143	264	31.7	24 7 25	4	13.2	18	1.34	440		20
539				31.9	24 56 37	1	11.1	1	-53	28		69
540	226	145	265	32.3	23 58 47	3	7.0	64	-01	5609		11
541				32.4	24 10 58	2	15.3	3	—14	2		23
542	227	144	266	32.4	23 47 44	1	2.9		—18	4925		0
543				32.6	24 32 41	2	15.3	2	-56	2		45
544				33.5	23 54 22	1	14.9	1	-34	4		7
545	228		267	33.5	23 38 40	3	14.1	10	-87	136	-94	9
546				34.1	24 14 59	4	15.2	9	-35	16	-54	27
547				34.3	24 46 16	2	14.2	4	-59	38	-72	58
548				34.6	24 29 8	1	15.0	3	-70	8		41
549				34.9	24 17 39	3	15.2	6	-44	14	-44	30
550				34.9	25 3 49	1	13.6	1	-90	14		76

## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p = 20$	Distance from Acyone
				m s	$^{\circ}$ ' "		m		m	$m^{-2}$		
551				41 35.0	25 0 55	1	14.0	1	.57	18		73
552	229		268	35.6	24 22 31	3	14.0	9	1.13	138	.94	35
553	231		269	36.3	23 39 23	3	14.2	9	.40	90	.19	8
554	230		270	36.5	24 11 39	4	13.8	17	1.29	226	1.24	24
555				37.0	23 8 31	2	15.3	2	.65	2		39
556				37.1	25 4 38	1	11.1	1	.23	28		77
557	232		271	37.1	23 22 8	5	13.5	14	.78	49	.42	25
558				37.7	23 57 5	1	15.3	1	1.72	2		9
559				37.8	23 52 10	1	14.9	1	.47	4		5
560	233	146	272	38.0	24 13 34	4	11.9	30	1.39	1066	1.53	26
561				38.3	23 33 32	1	15.5	1	1.45	2		14
562	234		273	38.6	23 54 22	3	13.7	17	1.04	221	1.05	7
563				39.3	22 46 37	1	14.7	1	1.04	2		61
564				39.4	24 16 2	1	14.9	1	.98	4		28
565				39.5	24 49 54	1	13.8	3	.08	55		62
566				39.6	24 4 22	1	15.3	1				17
567				40.5	25 0 15	1	13.3	1	.35	38		72
568		147		40.8	22 58 32	4	13.8	6	.67	88	.51	49
569	235	148	274	41.2	23 18 1	4	9.0	33	1.07	1816		30
570				41.4	24 46 28	3	13.3	7	.30	177	.73	59
571				41.7	24 58 35	1	14.4	1	—05	4		71
572				42.1	22 36 54	1	14.1	1	.34	4		71
573				42.5	24 52 23	1	13.3	1	.41	19		65
574				42.6	23 50 8	1	15.2	3	.93	6		3
575	238		275	42.7	23 9 34	2	15.1	2	1.22	6	1.08	38
576				42.9	24 46 30	3	13.7	7	1.05	108	.88	59
577	237	149	276	43.0	24 3 24	3	11.1	35	.38	1265	.31	16
578				43.1	23 59 34	1	14.9	1				12
579				43.1	25 1 40	1	11.4	1	—07	36		74
580	236	150	277	43.2	24 22 35	3	13.0	16	.28	417	.32	35
581				43.3	22 43 28	1	13.3	1	.29	14		64
582				43.3	24 48 0	2	15.2	2	1.39	4		60
583	240	151	278	43.5	23 41 36	3	12.0	28	1.17	1058	1.04	7
584				43.5	22 42 38	1	13.3	1	.05	14		65
585	239	152	279	43.6	23 50 25	4	12.7	28	.79	740	.80	4
586	241	153	280	44.0	23 49 44	5	12.5	29	.63	888	.83	3
587				44.7	24 59 13	1	15.0	1	.20	4		71
588	243		281	44.9	23 39 46	2	14.6	8	1.17	54	1.00	8
589				45.2	23 25 52	2	15.0	3	1.43	9		22
590				45.5	23 43 52	1	15.2	2	.93	1		5
591				45.7	23 37 25	1	14.8	2	.79	4		11
592	244	154	282	46.0	23 58 24	3	12.7	26	.40	818	.61	11
593				46.2	24 0 29	1	15.0	2	.46	5		13
594				46.3	24 21 43	3	15.2	5	.13	11	.24	34
595				46.4	23 23 18	1	15.5	1	1.85	1		25
596				46.6	22 48 13	1	12.6	1	—01	48	.12	59
597	245	155	283	46.8	23 14 5	4	9.7	23	.90	1191		34
598	242	156	284	46.9	24 22 24	3	13.7	12	.27	191	.07	35
599				47.0	22 37 16	1	12.6	1	.87	24		70
600				47.0	25 4 37	1	7.9	1	.09	44		77



## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_h$	$p$	$I_h$ Sh. and R. $p=20$	Distance from Alcyone
				m s	° ' "		m		m	m-2		
601				42 47.0	22 38' 8"	1	12.0	1	.07	58		69
602				47.1	24 58 38	1	11.1	1	.12	28		71
603				48.1	23 54 36	1	14.8	3	.85	14		8
604				49.7	23 24 46	1	15.2	2	.60	6		23
605				51.2	23 35 55	3	14.8	7	.95	28		13
606				51.6	23 56 30	1	14.7	2	.86	9		10
607	246		285	52.8	24 22 10	2	14.8	5	.41	28	.23	35
608			286	53.0	24 15 41	4	13.8	13	.62	222	.28	28
609				53.2	22 44 50	1	12.6	1	.46	48		63
610		157		53.2	22 54 35	3	11.5	9	.54	390	.19	53
611				53.3	24 33 25	2	15.2	4	.35	8	.51	46
612	247	158	287	53.6	24 3 31	3	12.7	21	1.04	658	.99	16
613				53.7	23 51 29	1	14.9	1	1.13	4		6
614				54.2	23 35 30	2	15.4	4	1.44	6		13
615				54.8	23 35 53	2	15.3	4	1.39	8		13
616				55.0	24 49 15	2	11.6	8	1.56	264		62
617			289	55.5	24 27 50	3	14.3	7	.43	60	.53	40
618	248		288	55.5	23 6 4	4	13.2	6	.53	126	.59	42
619				55.7	23 59 48	1	14.9	1	.14	4		13
620	249	159	290	56.0	23 37 59	3	10.2	38	.26	1679		11
621				56.7	24 47 41	2	13.4	5	.30	103	.31	60
622			293	56.9	23 41 24	3	14.5	7	.50	51		8
623			291	56.9	24 15 59	2	14.8	5	.68	20	.54	29
624	252		292	57.0	23 29 1	3	13.8	10	.48	152	.43	19
625				57.6	23 30 31	3	14.7	9	.40	26		18
626	259		294	58.1	23 30 50	3	13.9	9	.71	129	.74	18
627				58.2	24 13 2	2	14.8	9	.93	49		26
628	250		295	58.3	23 59 32	1	14.8	7	.57	39	.34	13
629				58.6	24 42 15	2	11.8	10	1.08	340	.99	55
630				58.7	24 10 47	1	15.3	1				24
631	254	160	296	58.8	24 27 17	3	13.5	9	1.10	172	.70	40
632				59.1	22 54 18	1	15.1	1			.32	53
633				59.2	23 53 47	1	14.7	2	.96	10		9
634	255		297	59.3	23 22 49	5	13.9	13	.96	138	1.03	25
635:	256	161	298	59.8	23 7 41	3	11.1	15	1.13	588		40
636	258	162	299	.0	23 23 14	5	12.0	22	.39	961	.13	25
637	251		300	.1	24 1 17	3	14.4	8	.55	56	.42	15
638	262		301	.2	23 26 4	3	14.5	8	.54	56	.16	22
639	257	163	302	.4	23 9 25	4	11.7	14	.45	602	.07	39
640:			303	.7	24 26 1	3	14.1	7	.49	56	.12	39
641:	253		304	.7	24 25 48	3	13.9	7	.61	80	.62	38
642	260		305	.7	23 16 59	4	13.6	10	.40	158	.29	31
643				1.4	24 52 41	2	13.2	2	.74	76		65
644:		165		1.4	22 53 1	3	10.8	10	1.35	359	.91	55
645:	263	164	306	1.5	23 7 31	3	12.7	10	.28	344	.19	41
646				1.5	24 25 25	3	15.1	5	1.35	9		38
647			307	1.6	23 40 49	2	14.2	9	.44	101	.34	10
648	261		308	1.8	23 16 42	3	14.6	9	1.45	46	1.03	32
649:				2.0	22 53 16	2	14.5	4	.57	13	.69	55
650				2.3	23 40 11	1	15.4	4	1.10	4		10

## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$mpg$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p = 20$	Distance from Alcyone
651:	264	166	309	m s 42 2.5	23° 47' 26"	2	m 10.4	39	m -31	m-2 1425		7'
652				2.6	24 17 13	2	15.4	3	-63	2		30
653				2.7	23 7 5	4	14.6	7	-12	29	-34	41
654:				2.8	23 47 25	1	12.6	1				7
655				2.9	23 41 5	1	15.7	3				10
656				3.1	25 2 1	1	10.9	1	-35	22		74
657				3.8	23 25 5	3	14.6	7	-33	32		24
658				4.7	25 2 26	1	15.0	1	-26	2		75
659	265	167	310	4.7	23 34 10	5	12.5	22	1.27	759	1.12	15
660	267		311	5.0	23 46 42	2	13.7	15	1.39	226	1.44	8
661	270	168	312	5.6	23 20 6	6	12.1	17	-29	707	-17	28
662				5.7	23 52 4	1	15.3	1	—03	2		9
663				5.9	24 17 28	2	15.0	3	1.05	8	-28	31
664				6.1	23 40 49	2	15.3	4	—34	5		10
665				7.0	25 1 4	1	13.3	1	-53	38		74
666	269	169	313	7.0	24 33 23	3	11.6	14	-27	563	—26	46
667				7.5	23 25 56	1	15.7	1				23
668				8.0	24 36 2	2	15.4	2	1.34	3	-46	49
669		170		8.0	24 40 46	2	8.4	16	1.43	1541		54
670				8.1	22 41 34	1	13.3	1	-40	14		66
671				8.3	23 40 38	1	15.3	1				11
672				8.4	24 58 55	1	14.4	1	—25	8		71
673	272		314	8.6	23 45 46	2	13.8	14	1.25	214	1.21	9
674				9.1	23 22 47	1	15.5	1	—34	2		26
675				9.2	25 1 43	1	13.6	1	-05	28		74
676				9.4	22 38 2	1	12.3	1	-26	28		70
677				9.4	23 58 46	1	15.4	2	—61	2		14
678	274	171	315	9.4	24 9 50	3	13.0	19	-54	583	-53	24
679				9.5	24 8 38	2	15.1	5	-37	14	-11	22
680	273	172	316	9.6	23 4 26	4	10.8	12	-79	507	-86	44
681	275	173	317	10.2	23 50 0	1	9.9	39	-27	1627		9
682	271	174	318	10.9	24 33 2	3	13.5	9	-31	184		46
683				11.0	22 41 56	1	12.6	1	—15	48		66
684	276		320	11.2	23 25 43	2	14.4	6	-52	58	-16	24
685	279	175	319	11.3	23 33 23	5	12.9	19	-43	490	-14	17
686				11.6	24 14 53	1	15.3	1				29
687	277	176	321	11.9	23 56 14	1	13.5	17	-41	340	-38	12
688				14.2	24 47 23	2	13.2	6	-27	151	-22	60
689				14.2	24 51 37	1	14.3	1	—40	4		64
690				14.3	24 18 7	1	15.3	1	—03	2		32
691				14.4	23 8 8	2	15.0	4	-66	10	-51	41
692				14.6	22 49 26	1	14.1	1	1.30	4		59
693	280	177	323	16.1	24 0 37	1	8.7	58	-17	3017		16
694	281		322	16.4	23 41 24	2	14.0	13	1.56	167	1.70	12
695				17.2	24 54 25	2	9.3	2	-24	129		67
696				18.0	23 16 10	1	15.5	1	1.73	2		33
697				18.4	23 58 30	1	15.3	1	1.09	2		15
698				18.6	24 44 23	2	11.6	9	-39	280	—08	57
699		178		18.6	22 56 41	3	12.5	7	-33	324	-32	52
700				18.8	22 37 23	1	11.7	1	-28	26		71

## General Catalogue (continued.)

No.	Wolf	Gaultier	Graf	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_h$	$p$	$I_h$ Sh. and R. $p=20$	Distance from Akyone
701:	283	179	324	m s 42 19.3	23° 20' 35"	5	13.1	13	1.00	398	.98	29
702	282		325	19.6	23 59 5	2	13.6	17	.32	292	.47	16
703				19.7	23 52 7	1	14.7	3	.52	16		12
704				19.9	22 51 46	1	14.1	1	.22	8	.09	57
705:				19.9	23 20 52	5	15.0	9	.82	35	.51	29
706	286	180	326	20.9	23 34 58	4	10.8	31	.35	1185	.42	17
707				21.2	24 19 22	1	14.3	1	.47	4		33
708	288	181	327	21.2	23 19 46	4	10.3	20	.24	958		30
709			328	21.2	23 47 14	2	15.2	4	1.68	8		11
710	284	182	329	21.4	24 32 17	2	12.1	11	.31	541	.01	46
711				21.4	24 52 59	2	13.2	2	.40	76		66
712	285		330	21.6	24 27 58	3	13.9	9	.62	124	.43	42
713	287		331	21.9	24 22 1	2	14.1	7	.50	86	.32	36
714				22.2	23 32 54	2	15.3	3	.44	8		19
715	289	183	332	22.6	23 45 11	2	13.3	16	1.00	383	1.14	12
716				23.3	24 48 56	2	14.0	3	.35	31		62
717	290	184	333	23.7	23 24 50	5	13.5	13	.37	251	.16	26
718				24.1	24 11 51	2	15.4	3	—03	6		27
719				24.6	24 34 20	1	15.9	1				48
720				24.8	23 45 29	1	15.4	2	1.70	2		12
721	291		335	25.6	24 33 9	2	13.7	6	1.17	142	1.11*)	47
722	293	185	334	25.6	23 6 50	3	5.3	22	—19	4182		43
723	292	186	336	26.2	24 34 13	2	11.2	15	.27	526	.01	48
724				26.5	25 1 2	1	8.6	1	.63	60		74
725				26.5	22 57 37	2	14.1	4	.78	20	.49	51
726				26.6	24 29 28	1	15.3	1	—05	2		43
727	294	187	337	27.2	23 17 2	4	13.6	11	.28	177	.13	33
728				27.4	23 53 53	1	15.2	3	.13	7		14
729				27.4	23 16 12	2	15.1	1	.58	2		34
730				27.9	24 41 11	2	12.5	8	1.07	290	.46	55
731				28.8	23 13 11	2	15.1	4	.17	10		37
732				29.1	25 0 46	1	15.0	1	.08	2		74
733	295	188	339	29.1	23 59 58	2	12.5	23	.17	796	.00	18
734	298		338	29.2	23 27 4	4	14.0	11	.70	129	.76	24
735	299	190	341	29.6	23 19 43	4	12.3	15	.41	629	.16	31
736	296	189	340	29.6	23 44 28	2	10.4	35	.28	1366		14
737				29.7	24 32 57	1	15.3	1	.47	2		47
738				30.6	25 1 30	1	12.6	1	.20	56		75
739				30.7	22 43 25	2	13.0	2	.30	52		65
740	302		342	31.9	23 47 3	2	14.0	10	.57	113	.48	14
741	297		343	32.0	24 33 55	2	13.9	6	.66	104	.56	48
742	300	191	344	32.6	24 2 17	3	7.2	61	.06	5286		20
743			345	32.7	24 7 20	3	13.4	13	.22	244	.00	24
744				33.0	22 59 37	3	13.5	5	.93	97	.66	50
745				33.2	23 21 34	2	15.2	2	—07	4		30
746	304		346	33.6	23 36 25	3	14.0	10	.26	98	.29	18
747	301	192	347	33.7	23 57 58	2	12.6	22	1.00	759	.92	17
748				34.0	23 38 35	2	15.1	5	.63	17		17
749				34.4	24 17 45	1	15.4	2	.64	3		33
750				34.8	23 36 7	1	15.5	7	.57	4		18

\*) It is assumed that Shapleys minutes of RA should be 33.2 instead of 32.2.



## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_\lambda$	$p$	$I_\lambda$ Sh. and R. $p=20$	Distance from Alicorne
751	303		348	<sup>m s</sup> 42 34.9	<sup>° ' "</sup> 24 20 59	3	<sup>m</sup> 13.3	9	<sup>m</sup> 26	<sup>m-2</sup> 218	.12	36
752				35.3	24 45 32	2	11.3	9	.20	286	—01	59
753	305		349	35.8	23 18 32	2	14.4	6	1.39	34	.98	32
754				36.0	25 1 25	1	10.3	1	.28	12		75
755	308		350	36.7	23 36 5	4	13.6	16	1.01	286	1.02	19
756	310		351	37.2	23 46 15	1	14.6	6	1.12	34	.96	15
757*	307	193	352	37.8	23 52 26	3	9.5	36	.23	1790		16
758				38.2	24 51 40	1	14.9	1	—32	2		66
759				39.0	24 34 7	2	14.4	4	.35	34	.46	49
760	312	194	353	39.1	23 7 41	3	10.6	20	.36	645		43
761	314	195	354	39.4	23 30 41	5	12.8	17	1.35	596	1.44	23
762				39.5	23 27 38	1	15.5	1				25
763	306		356	39.6	24 28 28	2	14.5	4	1.21	28	.98	43
764	311		355	39.7	23 54 44	3	13.7	16	.29	224	—16	17
765				40.3	22 42 56	1	13.3	1	.35	34		66
766				40.9	23 21 21	1	15.5	1	.62	2		31
767				41.2	24 28 17	1	15.9	1				43
768	313	196	357	41.5	24 22 29	3	12.4	13	.37	567	—03	38
769				41.6	24 48 53	2	14.4	2	—26	16		63
770	317	198	359	42.6	24 8 52	3	12.3	19	.19	726	.38	27
771	315	197	358	42.8	23 14 24	4	12.8	12	.44	443	.02	37
772	309		360	42.8	24 27 57	3	13.7	9	.33	152	.32	43
773		199		43.2	23 0 43	3	13.4	6	.39	113	.58	49
774				43.4	24 37 23	2	14.1	4	.24	52	.36	52
775	319	200	361	43.5	23 28 16	5	13.2	13	1.33	360	1.26	25
776:				43.7	24 1 28	1	15.7	1				21
777		201		44.8	22 59 31	3	12.5	7	.26	314	.18	51
778:	318	202	362	45.1	24 1 25	3	12.1	25	1.14	941	.98	22
779				45.5	24 10 31	3	14.2	8	.24	76	.08	28
780	321		363	45.5	23 28 26	5	13.9	13	.52	174	.43	26
781	320		365	46.0	24 0 56	3	14.7	11	1.15	54	.96	21
782				46.0	23 10 39	1	15.5	1				41
783				46.0	24 24 20	1	15.9	1				40
784	324		364	46.1	23 31 35	3	14.5	8	.46	41	.29	23
785				46.4	24 14 0	2	15.4	4	.22	8		31
786	316		366	46.8	24 23 42	3	14.5	7	.45	56	.24	40
787				47.4	23 50 11	1	15.3	1	.70	2		17
788	325	203	367	47.9	23 34 49	4	13.7	14	.27	253	.17	22
789	322		368	48.5	24 1 16	3	13.7	17	.12	258	.28	22
790:				48.7	22 52 59	2	13.7	2	.49	13	.99	57
791:				49.0	24 48 43	2	15.4	2	.40	1		63
792		204		49.0	22 57 13	3	8.3	13	.16	1048		53
793			369	49.2	23 50 30	3	14.4	7	.34	52	.39	18
794				49.2	24 0 52	2	15.5	6	.71	5		22
795				49.3	24 27 20	1	15.0	3	.37	12	.43	43
796:				49.3	24 48 48	2	13.5	2	.33	42		63
797	323		370	49.4	23 20 0	2	14.8	5	.99	14	.92	33
798				49.6	23 53 56	1	15.3	1	.06	2		19
799:				49.7	22 53 12	2	14.9	2	.44	1	.21	57
800				50.0	24 14 10	2	14.8	6	.50	28	.42	32

## General Catalogue (continued.)

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p=20$	Distance from Aleyone
				m s	° ' "		m		m	m-2		
801				43 50.3	24 42 59	2	12.9	6	.34	183	.26	58
802	327	205	371	50.3	23 13 5	4	11.4	18	1.24	568	1.01	39
803				50.8	23 38 35	2	14.7	4	.47	20		20
804				50.8	24 53 39	1	14.9	1				68
805	326	206	372	50.9	24 19 39	3	11.0	18	.22	701		37
806				51.0	24 25 8	2	14.6	3	.21	27	.43	41
807	328	207	373	51.7	23 57 39	3	11.6	29	.65	1055	.53	21
808	329	208	375	52.6	23 7 3	3	13.5	8	.34	156	.24	45
809	330		374	52.7	23 40 14	4	13.9	13	.93	168	.72	20
810				52.9	24 44 10	1	14.3	1	.34	8	.98	59
811				53.1	24 28 8	2	14.7	5	.82	36	.58	44
812				53.2	24 58 12	2	13.5	2	.25	28		73
813				54.0	23 10 23	1	15.5	1	1.72	1		42
814				54.1	23 52 32	1	15.3	1	.31	2		19
815	331		376	54.2	23 59 1	2	14.1	8	.44	66	.37	22
816				54.9	23 11 29	2	15.1	2	.22	4		41
817				55.4	24 28 1	2	15.1	4	.41	14	.71	44
818				55.6	23 32 22	2	15.2	2	.80	4		24
819:	332	209	377	56.4	24 14 18	4	13.1	13	.27	350		33
820				56.4	24 49 57	2	13.5	2	.33	56		65
821:				57.0	24 14 10	1	15.3	1				33
822				57.4	23 59 56	1	15.3	1	.31	2		23
823				57.5	23 29 28	2	15.5	2				27
824				57.6	23 19 29	2	14.9	2	.11	2		34
825				57.9	24 28 16	1	15.9	1				45
826	333	210	378	58.2	23 50 5	4	12.0	21	.34	875	.46	20
827	337	212	379	58.3	23 27 40	5	13.0	15	.28	407	.12	28
828	334	211	380	58.5	23 31 34	4	13.1	16	.49	374	.33	25
829				58.8	24 57 43	2	12.8	2	.30	96		72
830				58.9	23 29 4	3	14.7	8	.23	32	.61	27
831				58.9	24 17 47	1	14.9	1				36
832	335	213	381	59.5	23 43 1	3	12.6	20	1.16	631		20
833				59.6	24 47 49	1	15.3	1	.96	2		63
834				59.7	24 53 58	1	14.9	1	1.40	2		69
835				.3	24 44 54	2	14.2	2	.65	22	.52	60
836	338	214	382	.5	23 33 4	5	7.1	46	.20	4892		25
837:				1.0	24 52 59	2	13.5	2	.99	42		68
838	339		383	1.0	23 21 42	2	14.3	5	.69	32	.30	33
839:				1.3	24 53 5	2	14.0	2	.45	27		68
840				1.4	23 8 46	1	15.1	1				44
841	343		384	1.7	23 57 39	2	14.9	5	1.27	19	.82	23
842	341	215	385	3.2	23 34 45	5	13.2	16	1.21	435	1.33	24
843	340		386	3.4	24 24 24	3	14.3	7	.86	59	1.03	42
844				3.6	22 53 43	3	11.8	3	.65	134	.72	58
845:	336		387	3.9	23 39 4	2	15.4	3	1.12	9	1.09	23
846				4.1	24 44 34	1	15.3	1	.99	2		60
847				5.8	24 18 7	1	14.5	3	.45	30	.24	37
848				6.1	23 35 14	1	15.5	3	1.22	5		25
849				6.2	23 36 13	1	15.3	3	.10	8		24
850			388	6.3	23 45 13	3	13.6	14	.51	217	.88	22

## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_k$	$p$	$I_k$ Sh. and R. $p=20$	Distance from Alicorne
851		216		m s 43 7.3	22° 56' 49"	3	m 12.2	5	m -62	m-2 232	-52	55'
852				8.4	24 29 47	1	14.9	1	-75	4		47
853	342		389	8.5	24 5 29	4	14.2	9	-74	57	-81	28
854				9.1	24 25 34	1	14.4	2	1.04	22		44
855		217		9.1	23 1 44	3	13.4	5	-25	108	-53	51
856				9.4	23 34 33	1	15.3	1	-79	2		26
857				9.7	24 10 14	2	15.1	3	-52	12		32
858				9.7	23 43 54	2	15.0	6	-27	5	—12	23
859				9.9	24 25 6	1	14.9	1	-54	4		43
860				10.0	24 26 49	1	14.4	2	-25	22		45
861	345		391	10.0	23 20 53	4	13.9	9	-93	118	-96	35
862	347	218	390	10.1	23 28 30	4	11.4	22	-60	786	-66	29
863	346		392	10.4	23 39 37	4	14.0	11	-37	117	-47	24
864	344		393	10.9	23 42 14	4	13.7	13	-98	189	-99	23
865:				11.0	24 0 57	1	14.7	2	-37	8	—07	26
866				11.0	24 3 44	2	14.9	2	—42	8		28
867:	352		394	11.4	24 1 2	1	15.3	1	1.46	2	-74	26
868				12.5	23 40 50	1	15.9	1				24
869	355		395	12.6	23 19 29	2	14.8	5	-73	16	-41	36
870:	349	219	396	12.8	23 44 53	4	3.6		—22	4944		23
871				13.1	24 28 3	1	14.5	2	-33	22		46
872	357	221	398	13.5	23 33 41	5	12.6	17	-43	648	-43	27
873	351		399	13.5	23 16 18	2	14.5	6	-23	30	-37	39
874	348	222	400	13.6	24 4 45	4	12.5	22	-27	819		29
875	350	220	397	13.6	24 19 50	3	10.8	19	-30	811		39
876				13.8	22 57 43	3	13.9	4	-33	17	-30	55
877	354	223	401	14.1	23 18 22	4	10.9	20	-16	664	-07	37
878	353	224	402	14.4	23 49 52	4	4.9		—19	5052		23
879	356	225	403	14.6	23 55 47	4	12.6	16	-55	642	-51	25
880	359	226	404	15.1	23 13 25	4	12.6	12	1.01	521	1.32	41
881:				15.2	23 45 24	1	14.8	4	-99	4	1.18	24
882				15.4	24 26 34	1	14.7	2	1.01	20		45
883				15.6	24 53 58	1	14.3	1	-13	4		70
884		228		15.8	22 57 41	3	10.4	5	1.48	207		55
885	358	227	405	15.8	23 34 51	5	8.2	46	-11	3046		27
886	363		406	16.4	23 8 50	2	14.8	3	-43	6	-54	46
887	361	229	407	16.7	24 10 17	4	12.9	14	-24	418	-54	33
888				17.1	23 11 5	4	14.7	4	-77	10	-19	44
889	362	230	408	17.1	23 6 5	4	9.5	17	-23	1078		48
890				18.7	24 59 54	1	12.8	1	-06	24		76
891	365	231	409	19.1	24 5 26	4	7.6	54	-06	3895		30
892				19.8	23 52 35	1	15.3	1	-89	2		25
893:				20.2	23 45 43	2	14.9	5	-35	11	1.00	25
894:				20.3	23 45 38	1	15.7	2				25
895	364	232	410	20.3	24 6 31	4	12.2	17	-28	636	-53	31
896				20.9	24 53 18	2	13.2	2	-30	76		70
897				21.0	23 50 11	1	15.3	1	-61	2	-32	25
898				21.1	23 29 37	1	15.4	2	-67	4		31
899	366	234	412	21.9	24 28 17	3	13.3	8	-79	200	-87	48
900				22.0	24 55 7	1	14.9	1	-20	4		72



## General Catalogue (continued.)

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$mpg$	Number of images	$I_\lambda$	$p$	$I_\lambda$ Sh and R. $p=20$	Distance from Alcyone
				m s	° ' "		m		m	m <sup>-2</sup>		
901				43 22.0	23 37 14	3	15.1	5	.39	13		27
902	367	233	411	22.0	23 56 47	4	13.2	14	.90	423	.79	25
903				22.2	23 40 53	1	15.3	3	.41	8		26
904				23.3	24 38 8	1	15.3	1			.14	56
905	368	235	413	23.4	23 43 10	3	12.7	15	.19	457	.16	26
906				23.5	24 43 30	2	13.5	2	.32	42	.27	61
907				23.5	22 59 39	3	13.7	4	.45	26	.99	54
908	371		414	23.6	23 57 32	4	14.1	8	.43	72	.37	27
909				23.6	23 50 47	1	15.3	1	.58	2		26
910	370	236	415	24.0	24 4 32	4	6.6	51	—09	4749		30
911				24.1	24 33 50	1	14.9	1	—78	4		53
912				24.1	24 46 52	1	14.3	1	.01	8		64
913				24.1	24 26 38	1	15.3	1	1.66	2		46
914	374	237	416	24.2	23 17 18	4	13.7	11	.99	218	1.12	40
915				25.7	24 26 58	1	14.9	1	.26	4		47
916				25.9	24 33 52	2	14.3	3	.03	30	.21	53
917				26.1	23 54 32	1	14.9	1	.41	4		27
918	372		417	26.3	24 28 38	3	13.7	6	.79	91	.66	48
919	375		418	26.5	24 37 56	3	11.3	6	.72	153	.86	56
920	373		419	27.1	24 25 8	3	13.7	7	.52	105	.71	46
921				27.4	23 34 28	1	15.2	2	.75	6		29
922	378	238	420	27.7	23 32 4	4	11.8	17	.61	699	1.00	31
923	377		422	28.6	23 10 18	3	13.7	7	1.00	84	.81	44
924	376	239	421	28.9	23 56 33	4	8.1	44	.08	3180		28
925	381		423	28.9	23 29 22	4	14.1	10	1.19	99	1.93	32
926				28.9	24 13 25	1	15.3	1	—42	2		37
927	380	240	424	29.4	23 30 13	4	12.4	14	.93	543	1.19	32
928				30.1	23 54 40	1	15.3	1	1.20	2		28
929				30.4	24 16 11	1	15.3	1	.47	2		39
930	379	241	425	31.0	24 0 17	4	13.2	13	.58	312	.70	30
931				31.5	22 48 31	3	13.0	3	.61	47	.52	65
932				32.3	22 55 27	1	13.7	1	.46	4	.47	59
933			427	32.5	24 9 59	4	14.2	5	.35	50	.40	35
934	383		426	32.6	23 34 45	5	13.6	11	1.40	154	1.86	30
935				32.6	24 4 42	4	14.4	7	—02	35	.34	32
936	382	242	428	32.7	23 24 26	3	12.1	13	.62	607	.70	36
937			429	32.7	23 57 51	4	14.1	7	.41	61	.36	29
938				33.2	24 30 26	1	14.3	1	.11	8		51
939				33.3	24 10 20	3	14.8	3	.44	6	.31	36
940			430	33.5	24 28 59	2	14.2	2	.63	4	.64	50
941	385		431	35.0	24 21 5	3	13.6	7	.16	119	.47	43
942	384	243	432	35.3	24 19 23	2	11.0	15	1.17	651		42
943				35.8	22 58 28	3	13.4	3	.56	32	.64	57
944				36.3	24 42 39	1	15.3	1	—04	2		62
945	387		433	36.8	24 20 23	2	14.0	6	.48	62	.44	43
946	393	244	435	36.8	23 29 27	4	11.4	17	.45	660	.88	34
947	390		434	36.9	23 43 31	4	13.6	11	.42	182	.57	29
948	388	245	436	37.3	23 4 33	4	8.9	10	.18	867		52
949	391		437	38.3	23 46 29	4	13.8	9	.50	139	.47	29
950				38.4	24 35 12	1	14.3	1	1.35	8	1.32	55

## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p = 20$	Distance from Alcyone
951				m s 43 38.4	24 44 34	1	m 14.3	1	m -08	m <sup>-2</sup> 4	-41	64
952				38.7	23 47 45	1	15.2	2	1.28	1		29
953			439	38.9	24 11 53	3	14.1	5	-03	43	-13	38
954	389		438	39.0	23 57 11	4	13.9	12	-22	138	-28	30
955				39.0	23 23 32	2	14.8	4	-09	12		38
956	392	246	440	39.1	23 59 28	5	12.3	16	-74	708	-97	31
957				40.5	23 35 17	1	15.5	1	-04	2		32
958	396		441	40.6	23 9 53	4	13.9	7	-09	47	-04	48
959				41.0	24 24 16	1	15.3	1	-17	2		47
960	397		443	41.0	23 10 50	4	13.7	7	-46	67	-48	47
961	386		442	41.2	24 22 37	2	14.1	4	-51	48	-69	46
962	399	247	444	42.0	23 55 18	4	13.3	13	1.00	334	1.12	31
963	398		445	42.2	23 39 2	5	13.9	11	-29	137	-72	31
964				42.3	24 16 16	1	14.9	1	-44	4		41
965				42.4	23 46 22	2	15.4	2				30
966				43.5	24 52 37	1	14.9	1	1.41	2		71
967			446	43.6	24 7 38	4	14.0	6	-36	55	-04	36
968	395	249	447	43.7	24 6 35	4	12.6	9	-49	328	-60	35
969	400	248	448	43.8	23 43 55	4	11.7	19	-83	762	1.28	30
970	402		449	44.0	23 8 40	1	14.7	1	-01	1	-24	49
971				44.2	22 59 10	3	11.1	3	-32	112	-58	57
972	401	250	451	44.4	24 9 29	3	13.3	8	-97	166	-80	37
973	404		450	44.5	23 22 36	3	13.8	7	-28	85	-87	39
974				45.1	22 45 1	2	10.4	2	1.37	44		69
975	403	251	452	45.7	23 2 17	3	7.6	3	-12	727		55
976				46.7	24 23 53	1	14.3	1	-42	8		47
977	406	252	453	47.4	23 24 28	4	6.0	27	-12	4101		39
978	405	253	454	47.9	24 2 34	4	13.1	11	-68	299	-86	34
979				48.2	24 13 19	1	14.7	2	-43	11	-20	40
980	407	254	455	48.7	23 56 25	4	10.9	23	1.33	780	1.02	32
981				48.7	22 58 8	3	11.4	3	-33	136	-08	58
982				49.0	24 41 24	2	14.2	2	-78	26	1.06	62
983	408	255	456	49.5	23 28 34	4	11.7	14	-15	536	-27	37
984	409	256	457	50.0	23 26 25	4	11.8	13	-46	568	-62	38
985			458	50.6	23 49 38	3	14.2	7	-74	73	-32	32
986	413	257	459	54.1	23 24 5	4	12.3	13	-65	554	-51	40
987				54.3	23 44 53	1	14.9	3	-52	8		33
988	411	258	460	54.6	24 12 10	3	13.1	6	-49	206	-33	41
989	410		461	54.6	23 59 50	4	13.7	12	-25	188	-31	35
990				55.1	24 29 34	1	14.3	1	-31	8		53
991	416	259	462	56.7	23 43 29	4	13.3	11	-35	284	-50	33
992	412	260	463	57.0	24 2 10	5	13.2	11	-37	238	-64	36
993	415	261	464	57.5	23 54 49	4	9.1	31	-05	1767		34
994	417	262	465	57.7	23 13 34	3	11.0	11	1.17	457		48
995	414	264	466	58.9	24 17 1	3	13.4	6	-31	114	-14	44
996	418	263	467	58.9	24 2 40	4	7.4	24	-02	2631		37
997				59.0	22 52 47	1	13.7	1	-52	4		64
998::				59.2	23 32 37	1	15.4	1	-55	1		37
999:	420	265	468	44 -3	23 38 55	3	10.0	19	-21	841		35
1000:			469	-4	23 38 46	2	14.5	5	1.13	16	-86	35

## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p = 20$	Distance from Alcyone
				m s	° ' "		m		m	m-2		
1001::	421	266	470	44 8	23 32 37"	4	10.9	10	.30	258		37'
1002::	422		471	1.3	23 32 38	1	10.9	2				37
1003::	423	267	472	1.5	23 32 41	4	6.8	18	—03	2401		37
1004				1.5	22 53 14	1	14.7	1				64
1005				1.6	22 54 53	2	9.7	2	.18	26		63
1006	419	268	473	2.9	24 3 17	3	12.7	9	.23	340	.28	38
1007				3.4	23 53 4	3	14.2	7	.36	61	.51	35
1008	424		474	3.7	23 36 40	2	14.1	4	.54	42	.29	36
1009	425		475	4.6	23 6 45	2	13.4	2	.94	18	.92	54
1010				4.8	23 38 35	1	15.4	1	.63	1		36
1011				5.0	24 27 47	1	14.3	1	.22	8		53
1012				5.0	24 52 56	1	13.2	1	.58	38		74
1013	426	269	476	5.3	24 23 32	2	13.6	4	.32	73	.62	50
1014				5.5	24 49 2	1	12.5	1	.58	56		70
1015	428	270	477	5.9	24 21 59	2	12.6	6	.25	271	.39	49
1016	427		478	6.3	24 19 12	2	13.7	4	.76	63	.58	47
1017				6.7	24 1 35	1	15.0	1	.64	1		38
1018				8.4	24 56 23	1	15.3	1				77
1019				8.7	23 47 54	1	15.0	1	.28	2		36
1020*	429	271	479	8.8	23 54 39	3	11.8	14	.34	628	.41	36
1021				9.1	24 56 50	1	13.2	1	.27	19		78
1022	431	272	480	10.1	23 42 51	3	13.6	9	1.06	189	1.01	36
1023				10.1	23 59 37	1	14.6	1	.70	4	.49	38
1024	430	273	481	11.2	23 49 6	3	12.2	14	.88	623	1.17	36
1025				12.6	24 55 56	1	14.3	1	1.19	4		77
1026				12.6	23 50 27	2	14.9	4	.62	13	.82	37
1027	432	274	482	12.9	23 55 28	3	12.5	11	.99	542	1.24	37
1028			483	13.0	24 36 19	2	13.5	2	.40	36	.62	61
1029				13.4	23 38 25	1	15.3	2	.14	2		38
1030				14.2	24 13 46	1	15.0	2	.99	8	1.10	45
1031				14.4	23 59 29	1	14.8	2	1.10	10	1.08	39
1032	433	275	484	14.7	24 19 26	2	11.7	8	.26	343	—08	49
1033				14.8	24 9 54	3	14.0	4	.41	28	.27	43
1034	434		485	14.9	24 29 14	2	13.5	2	.51	32	.43	55
1035	437		487	15.8	23 30 59	2	13.7	6	.05	61	.33	41
1036			486	16.3	24 30 5	2	13.7	2	.46	22	.46	56
1037:	435		488	17.1	23 34 53	3	14.6	6	.65	14	.41	40
1038	436	276	489	17.2	24 21 42	2	9.2	11	.08	910		51
1039				17.3	23 46 38	1	15.0	1				38
1040:	439		490	17.9	23 34 52	3	13.9	6	.23	70	.11	40
1041				18.7	24 16 13	1	15.3	1	.78	1		47
1042	438		491	18.9	23 11 37	1	14.2	1	—06	2	.50	52
1043				18.9	24 55 9	1	13.9	1	.04	9		77
1044				19.4	24 38 56	2	13.4	2	.84	46		64
1045				19.4	24 46 42	1	14.3	1	.71	4	.12	70
1046				20.9	24 26 5	1	14.3	1	.46	8		54
1047				21.7	24 21 20	1	15.9	1				51
1048	442	277	492	22.9	24 10 14	3	12.8	8	.19	211	.04	45
1049	441	278	493	23.0	24 9 49	3	11.5	8	.47	298	.83	45
1050				23.2	24 0 13	1	15.0	3	—09	11	.41	41



## General Catalogue (continued.)

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_\lambda$	$p$	$I_\lambda$ Sh. and R. $p=20$	Distance from Alcyone
				m s	° ' "		m		m	m-2		
1051	444	279	495	44 23.4	23 34 39	4	13.2	8	.30	196	.14	41
1052			494	23.4	23 36 8	2	14.5	2	.67	6	.52	41
1053	445	280	496	23.5	23 38 57	2	13.1	7	1.21	247	1.34	40
1054				23.6	24 17 46	2	14.9	2	.26	6	.26	49
1055	443		497	23.7	23 30 18	3	14.1	5	.53	24	.41	43
1056	440		498	24.9	23 55 0	3	14.3	5	.78	28	.98	40
1057				26.2	24 10 28	1	15.3	1				46
1058				26.6	23 52 38	1	14.0	1	.95	4	.68	40
1059				26.7	22 47 39	2	11.2	2	.67	42		72
1060				26.7	23 51 46	1	15.0	1				40
1061				26.8	24 27 55	1	15.3	1				56
1062				27.1	23 34 11	1	14.5	2	.07	10	.12	42
1063	446		499	27.8	24 27 28	2	13.2	2	.99	56	1.12	56
1064:				28.3	24 21 11	2	15.2	2	1.00	2		52
1065				28.8	23 54 0	1	14.0	1	1.02	8		41
1066:			500	29.0	24 21 11	2	14.4	2	1.27	10	1.10	52
1067				29.1	23 0 31	1	13.3	1	.38	9	.77	62
1068				29.7	24 27 10	1	14.9	1				56
1069	447	281	501	30.0	24 11 31	3	7.2	16	.06	2129		47
1070	448	283	503	30.2	24 12 49	3	11.4	9	.27	391	.71	48
1071				30.2	24 14 46	1	15.3	5	.47	2		49
1072	450	282	502	30.3	24 2 37	2	12.8	6	.97	247	1.21	43
1073	452	284	504	30.6	23 16 8	3	11.4	6	.34	361	.30	52
1074				30.9	24 28 47	1	14.9	1	.40	4		58
1075	449		505	31.7	23 35 16	3	14.1	5	.40	38	.28	43
1076	451		507	32.0	24 32 3	2	12.3	2	.25	104	.32	60
1077	454	285	506	32.3	23 43 55	3	13.7	5	.29	77		41
1078				32.5	23 45 35	1	15.0	1	1.64	2		41
1079				33.3	24 49 38	1	13.9	1	.22	18		74
1080	453	286	508	33.6	24 12 18	3	11.1	9	.17	392	.18	48
1081			509	33.6	24 13 32	3	13.7	5	.65	49	.94	49
1082			512	34.9	24 33 55	1	13.9	1	.31	18	.41	62
1083				34.9	24 30 53	1	13.9	1	.23	18		60
1084				34.9	24 27 13	1	15.3	1				57
1085	455		511	35.0	23 52 37	3	14.1	5	.62	44	.32	42
1086				35.0	24 34 17	1	15.3	1	.44	1		62
1087	456		514	35.6	24 36 8	2	11.2	2	.37	88	.42	64
1088	457		513	35.6	24 29 16	2	10.1	4	.18	234		59
1089				35.7	23 27 44	1	15.5	1	.38	2		46
1090				36.1	23 57 5	3	13.2	5	.01	98	.18	43
1091	459		516	36.4	24 12 16	3	13.9	5	.93	66	.98	49
1092	458	287	515	36.4	24 2 35	2	11.2	9	.44	343	.32	45
1093				37.1	24 29 51	1	15.3	1				60
1094				38.0	22 57 10	2	13.6	2	.31	22	.48	66
1095				38.4	24 22 37	1	15.3	1	.86	2		55
1096				39.0	24 29 3	1	14.9	1				59
1097				39.2	23 58 4	3	14.3	4	.97	24	.58	44
1098				39.7	22 47 18	1	12.4	1	.11	24		74
1099				39.8	24 14 23	2	14.2	4	.07	24	.22	50
1100	460		517	40.6	23 11 26	3	12.7	3	1.05	71	1.32	56

## General Catalogue (continued.)

No.	Wolf	Gaultier	Graf	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_k$	$p$	$I_k$ Sh. and R. $p = 20$	Distance from Aleyone
				m s	° ' "		m		m	m <sup>-2</sup>		
1101				44 40.8	23 39 33	1	15.0	1	.95	1	.93	44
1102				41.2	24 18 1	1	14.9	1				53
1103	461	288	518	41.4	23 53 33	3	12.2	7	.22	361	.29	44
1104				41.4	23 48 57	1	15.0	1	.02	2		43
1105				41.4	22 56 29	2	13.4	2	.70	18	.29	67
1106	463	289	519	41.5	23 34 25	4	13.4	8	.37	158	.46	45
1107				42.4	22 55 4	2	13.4	2	1.06	18	.49	68
1108	464	290	520	43.3	23 37 50	2	10.6	10	.34	367		45
1109				43.6	24 29 4	1	14.9	1	.07	2		60
1110				44.1	24 17 1	3	13.7	3	.63	26	.80	53
1111				44.2	24 42 59	1	12.5	1	.61	56	1.07	70
1112				45.3	24 50 14	1	13.5	1	.16	14		76
1113			523	46.9	23 0 27	2	11.2	2	.83	42	1.10	65
1114			524	48.5	22 59 26	2	10.7	2	.15	55		66
1115				48.6	22 56 28	1	13.7	1	.63	4	.58	68
1116	468		525	48.8	23 4 53	1	14.7	1	1.10	2	1.00	62
1117				48.8	24 31 7	1	15.3	1				62
1118		291	526	50.1	24 8 16	3	13.3	3	.34	60	.31	50
1119				50.2	24 23 58	2	14.2	2	—0.4	9	.42	58
1120				50.3	24 15 35	2	14.4	2				53
1121	469	292	527	51.1	24 7 37	2	11.6	4	.95	259	1.04	50
1122				51.3	24 16 51	3	13.5	4	.61	40	.26	54
1123	470	293	528	51.6	23 33 11	4	13.2	5	.50	84	.14	48
1124	467		529	53.5	24 24 21	2	13.5	2	.75	36	1.10	59
1125				53.7	24 7 37	1	15.5	1				50
1126	471		530	53.9	23 7 15	3	11.4	3	.55	128	.27	61
1127	472	294	531	54.5	23 25 26	4	13.5	5	.32	55	.23	51
1128				54.8	23 26 47	1	14.6	1	1.25	2	.83*)	51
1129	473	295	532	55.4	23 39 35	2	7.1	9	.03	2533		47
1130				55.5	24 29 7	1	13.9	1				62
1131			533	56.1	23 1 40	2	12.8	2	1.36	28		65
1132	477	296	534	57.6	23 53 43	3	12.3	7	.75	326	.52	47
1133	479	297	535	57.6	23 31 59	4	12.2	6	.95	253	.69	49
1134	475		536	57.8	23 19 17	4	13.7	5	.45	31	.22	55
1135	478		538	58.6	24 32 38	2	12.4	2	.27	96	.46	65
1136				58.7	24 21 49	2	14.4	2	.85	5	.72	58
1137				58.8	23 1 30	1	14.7	1				66
1138	476		539	58.9	23 10 46	2	13.9	2	.72	11	.39	60
1139			537	59.0	24 14 43	3	13.2	3	.43	51	.31	54
1140			540	59.3	23 56 58	2	13.6	2	.60	22	.67	48
1141				59.5	22 51 8	1	8.8	5				74
1142			541	59.9	24 8 46	2	13.6	2	.60	26	.46	52
1143	474		542	45 .3	24 22 42	2	13.0	2	.13	66	.42	59
1144	480		543	.6	23 26 5	2	14.2	2	.51	4	.70	52
1145				1.3	23 59 45	1	15.0	1				49
1146				2.3	24 45 11	1	13.9	1	1.12	9	.79	75
1147			544	3.9	24 23 46	2	14.2	2	1.12	11	.87	60
1148			546	4.6	23 55 12	1	13.6	1	.49	18	.66	49
1149	481		545	4.7	24 2 28	2	13.6	2	.20	26	.27	51
1150	483	298	547	5.4	23 36 7	2	11.4	5	1.13	252		50

\*) Shapleys declination assumed to be 23° 26' 8" instead of 23° 26' 3".

## General Catalogue (continued.)

No.	Wolf	Gaultier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$mpg$	Number of images	$I_{\lambda}$	$p$	$I_{\lambda}$ Sh. and R. $p=20$	Distance from Aleyone
				m s	$^{\circ}$ ' "		m		m	m <sup>-2</sup>		
1151	482		548	45 5.3	24 38 12	2	12.1	2	.88	84	.97	70
1152				5.5	24 17 45	1	14.3	1	.77	4	.31	57
1153				5.5	24 39 11	1	14.9	1			.92	71
1154	486	299	549	6.1	23 39 20	2	13.3	3	1.08	105	1.25	50
1155			550	6.4	23 54 4	3	13.6	3	.32	41	.66	49
1156	484		552	7.1	24 22 21	2	12.3	2	.93	104	1.08	60
1157	489		553	7.3	23 48 34	2	13.8	3	1.11	31	1.00	49
1158	487		551	7.3	23 7 37	3	8.3	3	.07	182		63
1159				9.2	24 45 10	1	14.3	1	.85	4	.93	76
1160	488		554	9.6	24 3 18	1	13.6	1	1.05	18	1.25	52
1161	491	300	555	11.0	23 35 45	2	13.6	3	.59	55	.31	51
1162				12.1	23 55 40	1	14.9	1			.04	51
1163	485		556	12.6	24 26 52	2	13.2	2	.48	37	.50	64
1164	490		557	13.2	24 17 25	3	10.0	6	.96	117		59
1165				15.1	24 32 15	1	13.9	1	—63	9		68
1166	493		558	15.4	23 20 55	4	13.0	4	.29	70	.03	58
1167	492		559	15.4	24 12 59	2	12.5	3	.28	113	.04	57
1168	494		560	17.3	23 12 50	3	13.0	3	.69	23	.38	62
1169	496		561	19.1	23 19 14	3	9.6	3	.26	32		59
1170	497		563	20.1	23 31 32	3	13.4	3	.72	65	.59	54
1171	498		562	20.2	24 17 16	3	13.2	3	.00	51	.30	60
1172				21.2	23 55 5	1	15.0	1	.59	1	.48	53
1173				22.1	24 32 4	1	14.3	1	.68	4	.88	69
1174	499		564	22.2	24 4 49	2	11.5	4	1.11	166		55
1175:	500		565	24.5	24 33 38	2	11.7	2	.81	78	.83	70
1176				25.0	24 13 27	1	14.6	1	.77	4	.80	59
1177:				25.3	24 33 30	2	14.5	2	.21	4	.61	70
1178	501		566	25.5	24 21 54	2	13.2	2	.44	28	.42	63
1179				26.0	23 59 29	1	15.0	1	.28	2		55
1180	502		567	27.1	23 23 44	2	13.7	2	.56	13	.31	59
1181				27.1	23 47 11	1	14.0	1	1.38	8	1.00	54
1182	506		569	28.3	23 39 25	2	13.0	2	1.10	66	.97	55
1183	504		568	28.5	23 28 56	1	14.6	1	1.90	4	1.11	57
1184	503		570	28.6	24 13 4	2	9.0	2	.11	108		60
1185				29.1	24 25 4	1	13.9	1	.22	9	.42	66
1186	505		571	29.3	24 15 44	2	11.8	2	.20	114	.38	61
1187:				30.4	24 0 32	1	15.1	1				56
1188				30.7	23 33 25	1	14.0	1	.48	8	.67	56
1189:				30.8	24 0 38	1	14.9	1				56
1190	509		573	30.9	23 37 28	2	12.4	2	.96	96	.64	55
1191:				31.9	23 32 2	1	12.9	2				57
1192:	512		574	32.1	23 32 1	1	12.5	2	.22	80		57
1193				33.0	23 54 16	1	14.0	1	—04	8	.58	55
1194				33.2	23 35 58	1	14.6	1	.65	4	.99	56
1195	507		575	33.6	24 18 59	1	15.1	1			1.15	63
1196				34.6	24 11 2	1	14.6	1			.32	60
1197	511		576	34.8	24 18 38	1	13.2	1	.50	9	.32	63
1198				34.9	23 37 24	1	15.0	1	—31	1		56
1199	513		577	35.0	23 44 0	2	12.8	2	.87	76		56
1200	515		578	35.3	23 20 11	1	13.9	1	—35	4	.24	62



## General Catalogue (continued.)

No.	Wolf	Gautier	Graff	$\alpha$ (1900) 3h	$\delta$ (1900)	Number of plates	$m_{pg}$	Number of images	$I_k$	$p$	$I_k$ Sh. and R. $p=20$	Distance from Alcyone
				m s	° ' "		m		m	m <sup>-2</sup>		
1201				45 35.6	23 49 53"	3	13.7	3	.37	31	.29	56
1202	516		579	35.6	23 36 40	2	12.3	2	.59	104	.59	57
1203				37.1	23 42 50	1	15.0	1				56
1204				39.4	23 44 44	1	15.0	1	1.28	2		57
1205				40.4	24 10 27	1	14.4	1			.51	61
1206	518		580	40.5	24 14 53	2	12.7	2	.67	76	.42	63
1207	519		581	41.8	24 22 2	1	12.1	1	.26	48	.54	66
1208				42.1	23 42 40	1	14.6	1	.47	4		57
1209	521		582	44.6	24 15 1	2	12.7	2	.16	38	—01	64
1210	520		583	44.7	24 25 45	1	11.8	1	.27	56		69
1211	522		584	47.1	24 25 31	1	12.8	1	1.35	28	1.59	69
1212				49.3	24 19 28	1	13.6	1	—36	4	.04	67
1213				49.4	24 3 41	1	14.0	1	1.07	8	.80	61
1214				49.7	23 55 28	1	14.0	1	.05	8	.14	59
1215	524			50.9	23 27 7	2	13.1	2	.22	28		63
1216	526			51.3	23 41 8	1	14.0	1	1.22	8		60
1217	527			55.0	23 56 5	2	12.8	2	.14	38	—11	61
1218	528			55.2	24 5 14	2	13.2	2	.81	23		63
1219				56.9	24 0 49	1	14.0	1	.45	4		62
1220	530			57.4	23 54 43	1	13.6	1	1.10	18		61
1221	533			58.4	23 51 55	1	12.9	1	.47	38		61
1222	534			58.4	23 58 44	2	11.5	2	.25	110		62
1223	537			59.8	23 31 23	2	13.5	2	.09	18		63
1224	535			59.9	23 36 10	2	9.7	2	.31	40		62
1225				.9	23 59 47	1	14.6	1				63
1226				1.6	23 42 42	1	15.0	1	—18	1		62
1227				1.8	24 11 49	1	14.0	1	.95	4		66
1228	538			2.0	23 47 8	1	13.6	1	.54	18		62
1229	539			2.8	24 10 40	2	12.8	2	.38	33		66
1230	540			3.0	24 21 50	1	12.5	1	.92	19		71
1231	541			3.9	23 51 23	1	12.9	1	.35	38		62
1232	547		46	7.6	24 1 41	2	13.0	2	.33	56		64
1233	550			10.4	23 55 47	1	10.5	1	.57	22		64
1234	548			11.3	23 42 29	1	13.6	1	.45	9		64
1235	553			14.4	24 1 47	2	12.3	2	.84	75		66
1236	554			18.7	23 45 5	1	13.2	1	.82	28		66
1237	559			18.8	24 6 2	2	10.7	2	.84	64		68
1238	562			27.2	23 51 7	1	14.0	1	1.52	8		68
1239	563			29.6	23 33 46	1	11.3	1	1.12	44		69
1240	568			32.4	23 37 53	1	13.2	1	.47	28		69
1241				34.3	24 2 1	1	13.6	1	.46	9		70
1242				48.2	23 58 50	1	13.2	1	.89	28		73
1243				53.8	23 50 38	1	13.6	1	.18	9		74
1244				54.3	23 37 26	1	13.6	1				74
1245				59.2	23 51 29	1	12.9	1	.30	19		75
1246				47 3.0	23 48 56	1	12.9	1				76

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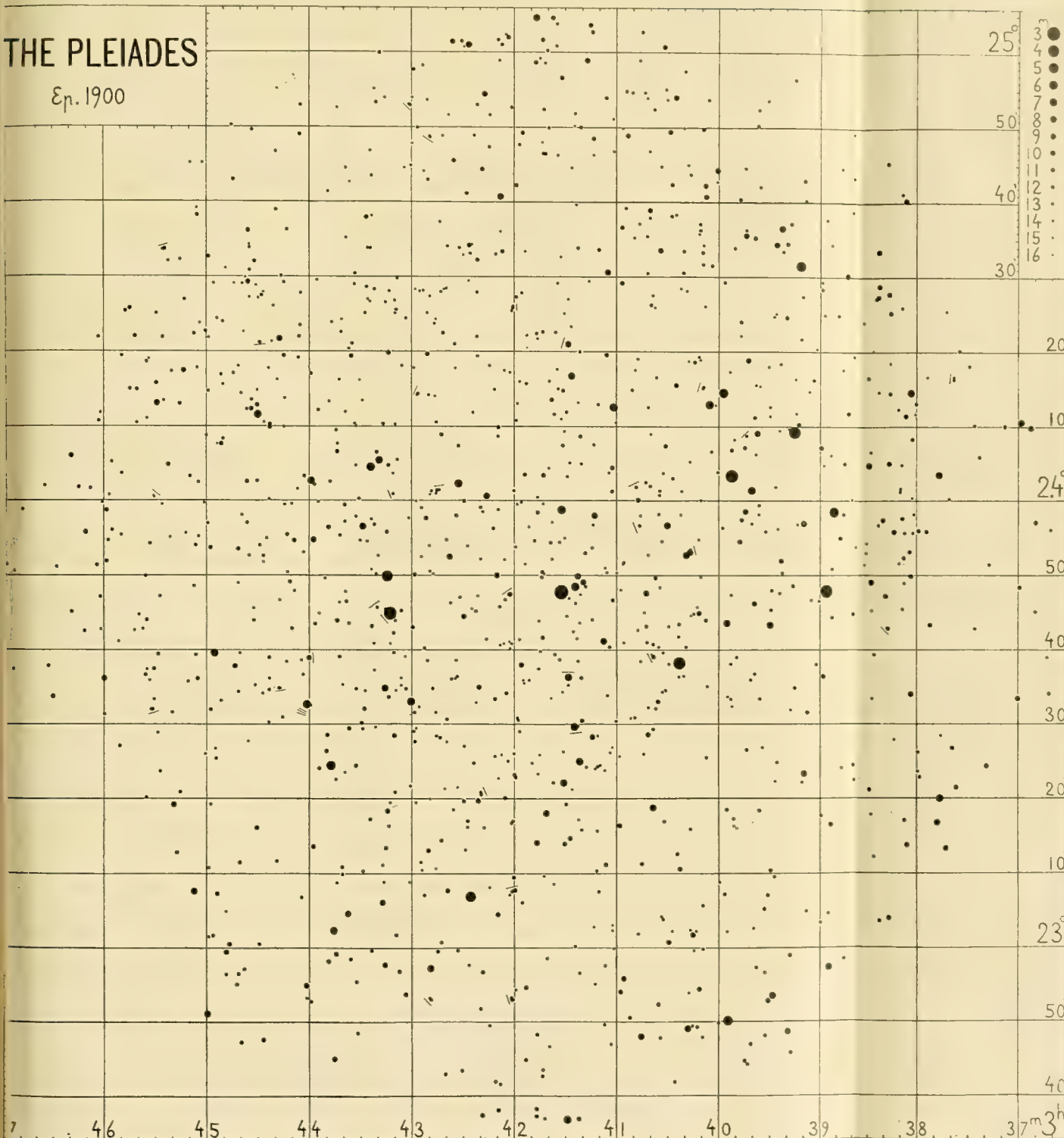




## THE PLEIADES

Ep. 1900

25° 3' ●  
 4' ●  
 5' ●  
 6' ●  
 7' ●  
 8' ●  
 50 9' ●  
 10' ●  
 11' ●  
 40 12' ●  
 13' ●  
 14' ●  
 15' ●  
 30 16' ●  
 20  
 10  
 24°  
 50  
 40  
 30  
 20  
 10  
 23°  
 50  
 40  
 37<sup>m</sup> 3<sup>h</sup>





ON  
THE QUANTUM THEORY  
OF LINE-SPECTRA

BY

N. B O H R

---

PART I

---

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATH. AFD., 8. RÆKKE, IV. 1, 1.



KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL

BIANCO LUNOS BOGTRYKKERI

1918

Pris: 2 Kr. 25 Øre.







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ON  
THE QUANTUM THEORY  
OF LINE-SPECTRA

BY

N. B O H R

---

PART II

---

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATH. AFD., 8. RÆKKE, IV. 1, 2.

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KØBENHAVN

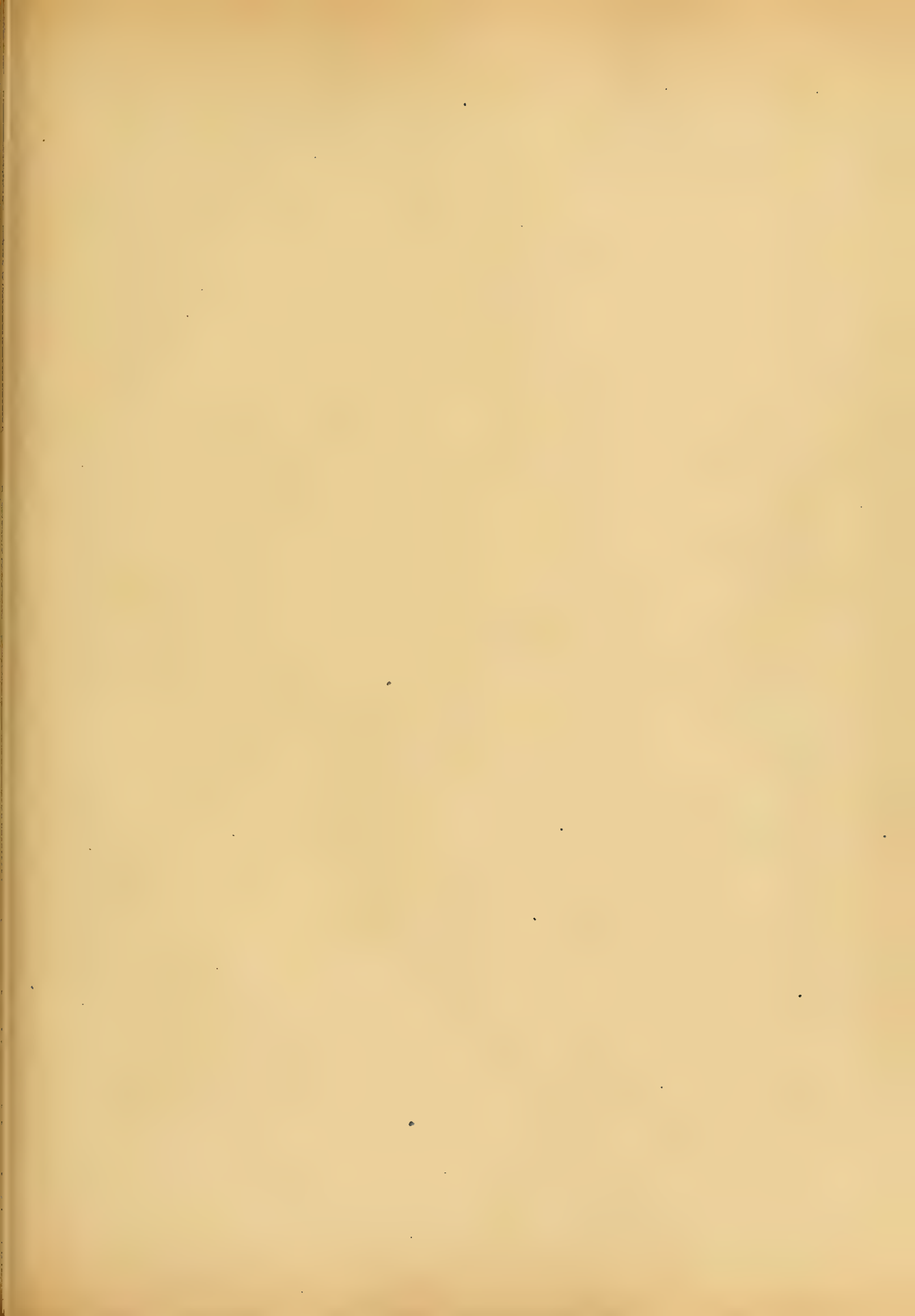
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BIANCO LUNOS BOGTRYKKERI

1918

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BY

N. BOHR

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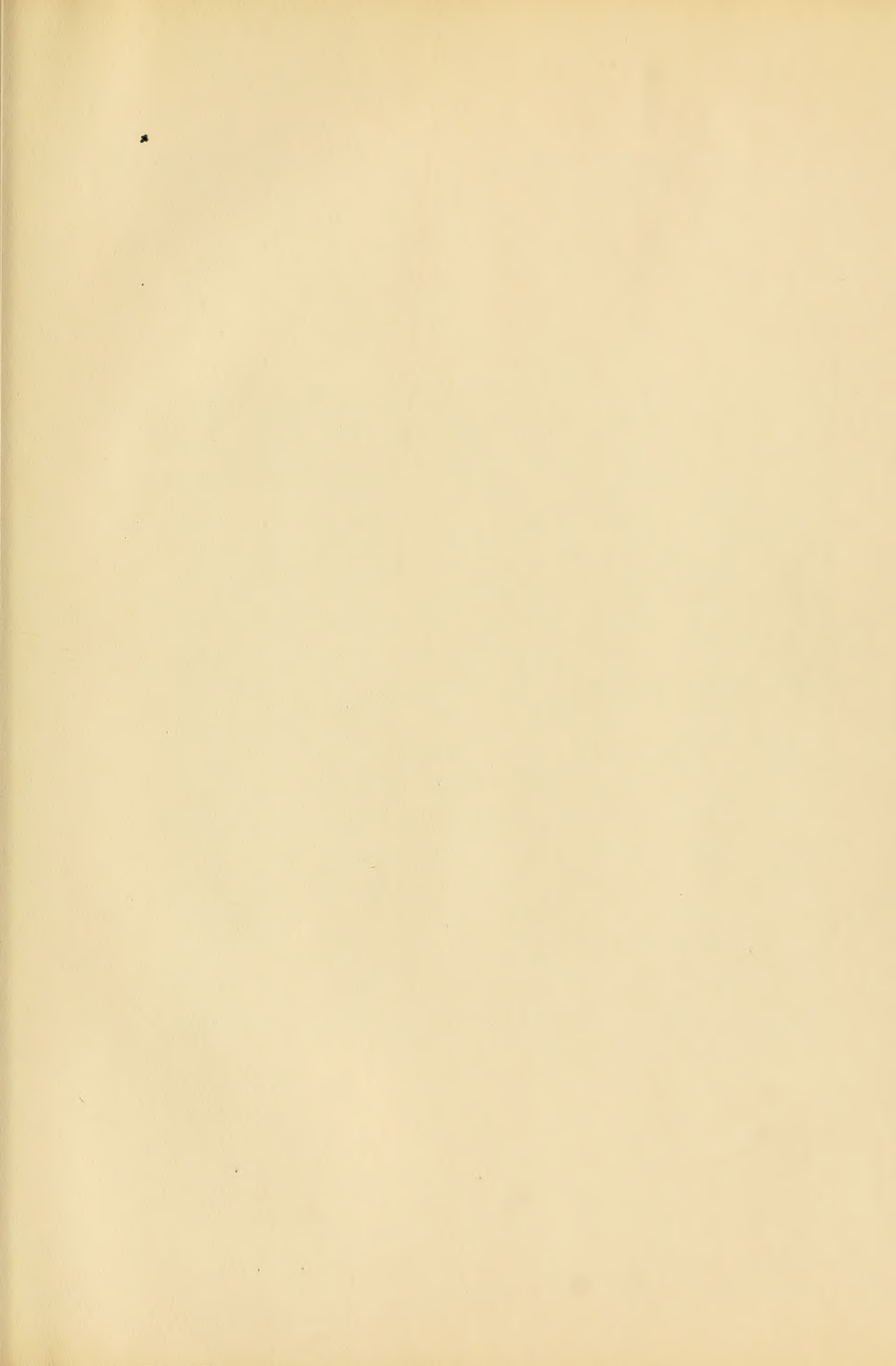
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